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A genetic evaluation of calving traits in the United Kingdom

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Dedication

This thesis is dedicated to my parents for their unconditional love and support.

They have always encouraged me to fly and to enjoy the journey.

To Bernadette Eaglen-Oosterbroek and Malcolm Eaglen.

Declaration

I declare that I have composed the present thesis. This is my own work and any assistance has been duly acknowledged. The work described has not been submitted for any other degree or professional qualification.

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Notation key

Commonly used abbreviations are given here. Specific abbreviations to this thesis and the separate chapters are given within each chapter.

CE: Calving ease
CEd: Direct calving ease
CEm: Maternal calving ease
SB: Stillbirth
GL: Gestation length
GLd: Direct gestation length
GLm: Maternal gestation length
UK: United Kingdom
PTA: Predicted transmitting ability
PLI: Profitable Lifetime Index
CIS: Cattle Information Service
NMR: National Milk Records
Mgs: Maternal grandsire
TBV: Total breeding value
SNP: Single Nucleotide Polymorphism
DGV: Direct genomic value
BLUP: Best linear Unbiased Prediction
CI: Calving interval
NR56: Non-return after 56 days
NRINS: Number of inseminations
DFS: Days to first service
SCC: Somatic cell count
DIM: Days in milk
EBV: Estimated breeding value

s.e.: standard error

Abstract

The consequences of complications during calving are currently costing the UK dairy cattle industry approximately £110 for a calving of moderate difficulty and £400 for one that is severe. With incidences of difficult first calvings reaching 24% and 4% for a moderate and severe difficult calving respectively, reducing calving complications would be of great benefit to the UK dairy cattle industry. This PhD evaluates (i) the importance, (ii) the most optimal way, and (iii) the potential consequences of genetically selecting for two main traits associated with calving complications, calving ease (CE) and stillbirth (SB). For this, approximately 50.000 first parity and 300.000 later parity national calving data records were kindly provided by two major milk recording organisations in the UK. The work carried out shows that detrimental effects following a difficult first calving are long-lasting as subsequent performance of both the dam and the calf involved is worsened. Fertility of the dam is negatively affected by a difficult calving resulting in an increased calving interval and decreased ability to conceive. A reduction in milk production of a veterinary assisted dam, compared to a non-assisted dam, was detected in the first part of lactation. Veterinary assisted born calves showed a significantly lower milk yield, compared to farmer assisted calves, throughout their first lactation as adult heifers suggesting that the physiological effects, or causes underlying a difficult birth, are long lived. The study advises that genetic parameters of calving traits are to be estimated with an extended sire multi-trait model (accuracy vs. practicality). On average, direct and maternal heritabilities for calving traits are low. A highly heritable indicator trait such as gestation length (GL) can aid in the estimation of genetic parameters for CE and SB although genetic correlations of these traits with

GL are moderate. A significant negative genetic direct-maternal correlation was found for CE in first parity recommending farmers to consider both direct and maternal genetic merit for CE when making a selection decision. CE and SB are highly positively correlated traits. GL is maternally correlated to SB in first parity and directly to CE in later parities, both correlations are positive. Estimated genetic correlations with other important traits in dairy cattle breeding show that CE and GL are both directly and maternally related to important selection traits which need to be taken into account if implementation into breeding indices occurs. Results advise limiting the use of GL to benefit the prediction of parameters for low heritable calving traits rather than selecting on GL itself. Genetic correlations suggest that individuals born easily are genetically prone to high milk yield and have reduced fertility in first lactation. Difficult calving heifers are likely to be associated with being wide and deep and high producing animals with a reduced ability to subsequently conceive. Individuals that are born relatively early are associated with good genetic merit for milk production. And finally, individuals carrying their young longer are genetically associated with being wide and large animals that were born relatively early themselves. Lastly, an extension of the current univariate genomic model to a bivariate model, which allows for a possible genetic direct-maternal covariance, shows that improvement in accuracy of genomic breeding values can be gained from use of a bivariate genomic model for maternal traits such as CE. Further development of the model is however recommended prior to the publication of genomic proofs for CE or any other maternal trait. Genetic selection can serve as a tool in the reduction of difficult calvings. The results of this thesis serve to let this happen in a controlled and sustainable manner.

Publications

Research articles (peer-reviewed)

Eaglen S.A.E., Coffey M.P., Woolliams J.A., Mrode R,. Wall E. 2011. Effect of calving ease on the phenotypic performance of dam and calf in UK Holstein-Friesian heifers. J. Dairy. Sci., 11**:**5413-5423

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Eaglen S.A.E., Coffey M.P., Woolliams J.A., Wall E., Mrode R. 2012. Improvement of the genomic model for direct and maternal calving ease in the UK. International Conference on Quantitative Genetics, Edinburgh, United Kingdom, June 2012. p197

Eaglen S.A.E., Coffey M.P., Woolliams J.A. and Wall E. 2012. How direct and maternal gestation length genetically relate to fertility, milk production, type and lifespan in UK Holstein-Friesian heifers. British Society of Animal Science, Nottingham, United Kingdom, April 2012. p40

Eaglen S.A.E., Coffey M.P., Woolliams J.A. and Wall E. 2011. The direct and maternal genetic relationships between calving ease, gestation length, milk production and selected type traits. Interbull Annual Meeting, Stavanger, Norway, August 2011

Eaglen S.A.E., Coffey M.P., Woolliams J.A., Wall E. 2011. Direct and maternal genetic relationships between calving ease, fertility, production and somatic cell count in UK Holstein-Friesian heifers. European Federation of Animal Science, Stavanger, Norway, August 2011. p109

Eaglen S.A.E., Coffey M.P., Woolliams J.A. and Wall E. 2011. Genetic correlations between calving ease and fertility traits in UK Holstein Friesian heifers British Society of Animal Science, Nottingham, United Kingdom, April 2011. p14

Eaglen S.A.E., Coffey M.P., Woolliams J.A. and Wall E. 2011. Estimated genetic parameters of calving ease and stillbirth in UK Holstein-Friesian cattle, using a multi-trait animal model. British Society of Animal Science, Nottingham, United Kingdom, April 2011. p210

Eaglen S.A.E., Coffey M.P., Banos G., Woolliams J.A. and Wall E. 2010. Analysis of calving traits and gestation length in UK Holstein heifers using an animal model. World Congress on Genetic Applied to Livestock Production, Leipzig, Germany, August 2010, 0599

Eaglen S.A.E., Coffey M.P., Woolliams J.A., Mrode R,. Wall E. 2010. Effect of calving ease on the subsequent performance of cow and calf in UK Holstein-Friesian cattle. British Society of Animal Science, Belfast, United Kingdom, April 2010. p164

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CHAPTER 1:

General Introduction

1.1. Breeding for functional traits in dairy cattle

During the last few decades, the dairy cattle industry has steadily moved from the historical focus on milk production to a more holistic focus which is putting emphasis on functional traits alongside production traits. The main reason for this shift was the growing awareness that in order to sustain economic efficiency, breeding should not only target increases in income but also reduction of costs (Mark, 2004). Furthermore, the development of more sophisticated genetic evaluation methods led to the discovery of the negative genetic relationships between production and functional traits which made it essential for functional traits to be included in national breeding indices to stop undesirable genetic trends in correlated traits. With the exception of the Scandinavian countries, whose selection indices already included health and reproduction traits, this has led to a world-wide growing interest in broadening breeding goals. Today, an ever increasing number of traits are being subjected to genetic evaluation (Mark, 2004; Windig et al., 2010).

Since 1995, selection indexes for dairy breeding in the UK have evolved. Inclusion of longevity (1995, ITEM index), somatic cell count (SCC) and type traits (2003) and fertility traits (2006) have led to the current Production Lifetime index (£PLI index). In 2007, PLI was revised and further emphasis was put on health, welfare, and fitness traits so that the emphasis on production was reduced from 75% in 2003 to 45% (Miglior et al., 2005; DairyCo, 2012; Wall et al., 2011). In 2009, PLI was again revisited for the potential inclusion of three more traits, each representing a current problem among dairy cows in the UK. The project was entitled 'Expanding Indices' and involved six industry partners, namely the Cattle Information Service (CIS), Cogent, DairyCo, Genus, Holstein UK and National Milk Records (NMR),

who have an interest in the welfare, health and sustainability of dairy systems. The key traits of interest had been identified as calving ease, udder health and longevity. The results of this PhD project have largely fed into the calving ease section of the 'Expanding Indices' project. The focus throughout the thesis is therefore highly applied.

1.1.1. Calving traits as selection traits

The importance of calving traits for the dairy cattle industry is clear. Calving marks the start of lactation and supplies the herd with replacement animals. It is therefore a key event on a dairy cattle farm and essential for the sustainability of the herd. Biologically, parturition is a collaboration between mother and offspring. Onset of parturition initiates precisely timed endocrine changes that trigger a sequence of physiological events in both individuals (Senger, 2003). Considering the complexity and importance of the parturition process it comes as no surprise that complications during calving have potential consequences for both animals and farms. Indeed, numerous studies have confirmed the detrimental effect of poor calving performance on the dairy industry. Economically, difficult calvings are associated with high labour and veterinary costs, reduced performance and loss of animals (Meijering, 1983). In the field of animal welfare, difficulty at parturition (dystocia) is ranked one of the most painful conditions of cattle (Huxley and Way, 2006).

Calving traits are generally represented by two main traits that are involved with the calving process: calving ease (CE) and stillbirth (SB) (Meijering, 1983). Calving ease provides a measure of the amount of assistance given during calving which is assumed to be highly correlated to the ease of the parturition process. Stillbirth is defined in the UK as calf mortality at, or within 48 hours after, birth. The focus of

this thesis thus lies mainly on the evaluation of CE and SB although in parts, gestation length (time from conception to calving) will also be indicated as a calf performance trait. If so, then this is pointed out.

Genetically, there is genetic variation in calving traits and so genetic selection is feasible, even though heritabilities are low (Dekkers, 1994). Under some assumptions, complications at calving are currently costing the UK dairy cattle industry approximately £110 for a calving of moderate difficulty and £400 for one that is severe (McGuirk et al., 1998). Hence, calving traits are of economic importance and thus, if genetic selection can aid in reducing the incidence of calving complications, this would be of economic benefit to the dairy cattle industry.

1.2. National recording of calving traits in the UK – Data description

This thesis utilised nationally recorded data on calf performance. The data provided was edited subject to each research objective and thus datasets differ in size and structure between Chapters. Specific data edits are described per Chapter. This section serves as an introduction to the general dataset that was available for this PhD project and lists major data edits which were consistent throughout the thesis.

1.2.1. Recording of calving traits

Data for this thesis was collected from 1995 to 2009 and kindly provided by two milk recording organizations in the UK; the Cattle Information Service (CIS) and National Milk Records (NMR). Calving performance data is routinely collected by CIS as part of their progeny testing programme, whereas the data from NMR is farmer recorded.

Calving ease is generally scored on a categorical scale designed to be practical yet minimising room for subjective interpretation. The number and definitions of scale categories differed between the two data sources although both scales ascend in calving difficulty, hence a higher score reflects more difficulty. Scoring was conducted according to a 4-grade scale by CIS: 1- easy, 2- assisted, 3-difficult, and 4- vet assisted while NMR scored according to a 5-grade scale: 1- normal (not assisted), 2- moderate assistance (farmer), 3- moderate assistance (vet called as precaution) 4- difficult (extraction by farm staff), and 5- very difficult calving (vet assisted). To harmonise the different scales, in order to reach a unified scoring system for data analyses, categories 2 and 3 of the scale used by NMR were merged; both referring to 'moderate assistance required' and the latter holding a very small frequency of the data (0.43%). Thus, calving difficulty scores throughout this thesis were categorised as: 1- easy (non-assisted), 2- moderate farmer assisted (vet called as precaution) , 3-difficult farmer assisted, and 4- very difficult vet assisted. Stillbirth is defined in the UK as calf mortality at or within 48 hours after birth. It is a binary trait and therefore scored on a 0-1 scale where 0 represents a living calf as 1 stands for a stillborn calf in both data sources. In addition, NMR registers the sex of the stillborn calf whereas CIS chooses not to. Incidences of CE and SB within parity, sex and data source can be found in Table 1.1

Frequency distributions differed across the two data sources (Table 1.1). To account for these differences the scored CE scores (1-4) were transformed to values on the underlying normal distribution (average liability value) within data source and parity prior to any genetic analyses.

Table 1.1 Calving ease and stillbirth incidences within parity, data source and sex of calf

		Parity			Data source		Sex of calf	
		1	2	≥3	CIS	NMR	Male	Female
CE[1]								
	1	74.17%	85.10%	85.08%	86.07%	82.56%	80.69%	86.89%
	2	22.86%	13.00%	13.03%	11.94%	15.14%	16.57%	11.85%
	3	3.22%	1.51%	1.42%	1.41%	1.78%	2.19%	0.97%
	4	0.74%	0.39%	0.46%	0.57%	0.43%	0.55%	0.28%
SB[2]								
	0	92%	95%	95%	95%	96%	94%	97%
	1	8%	5%	5%	5%	4%	6%	3%

[1] CE = Calving Ease; 1 = easy (non-assisted), 2 = moderate, farmer assistance, 3 = difficult, farmer assistance, 4 = very difficult with veterinary assistance
[2] SB = Stillbirth; 0 = living, 1 = stillborn

1.2.2. Dataset composition

In total, 373,888 calving trait records were used in this PhD project, originating from 6,573 herds across the UK. Data consisted of single calvings only i.e. no twins. All data was on Holstein-Friesian dairy cattle, thus breed of sires and dams were therefore required to be Holstein, Friesian or Holstein-Friesian. The data represented 16,372 bulls of which 5,656 bulls appeared as service sire, 15,314 bulls as maternal grandsires (mgs) and 4,598 bulls appeared as both service sire and mgs (Table 1.2). Data consisted of performance records across five lactations, with the least number of records associated with first parity (Table 1.2). 23,149 dams were recorded at both birth and calving which is 7.8% of all recorded animals (phenotype for both birth and calving). The age of dam ranged in total from 18-202 months, age of dam in first parity ranged from 18-48 months. The sex ratio of the calves varied within parities but showed a 50%-50% ratio in later parities (Table 1.2). Gestation length was restricted to 265-295 days prior to analyses for national genetic evaluation purposes. The distribution of gestation length in the dataset is shown by parity in Figure 1.1.

Additional variables available for analyses were: date of insemination, date of calving, year of birth of the dam, year of birth of the sire, year of birth of the mgs, and calf size. The latter, calf size, was scored on a categorical scale of three scores: small, normal and large.

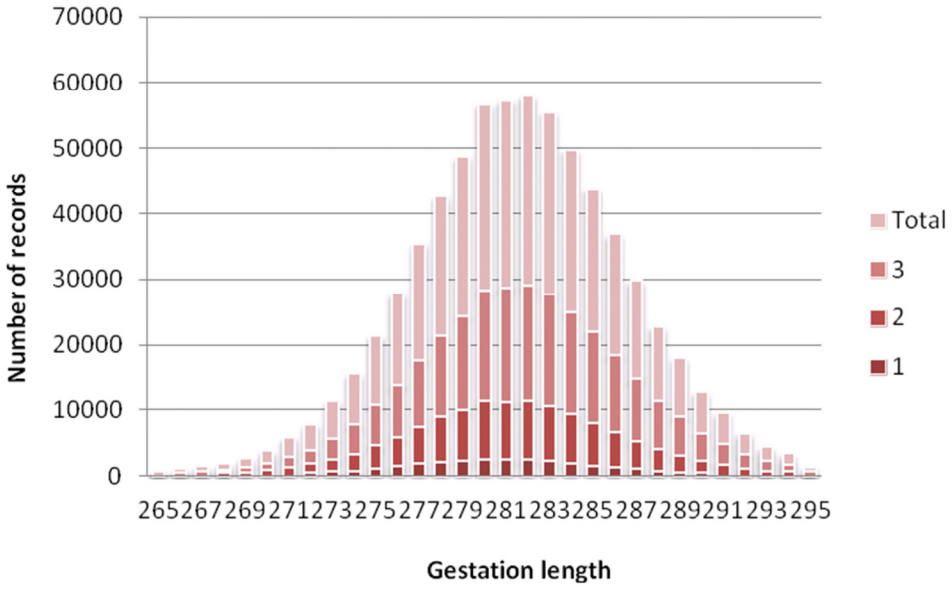


Figure 1.1 Distribution of gestation length per parity

Table 1.2 Descriptive statistics of the data

	Parity			
	1	2	≥3	Total
Records	43135	110498	220255	373888
Dams	43135	110498	177874	294370
Sires	3345	4057	4635	5656
Mgs	4879	8956	12565	15314
Herds	2824	5702	6224	6573
Dams with birth record	2016	2397	4148	23149
NMR	19899	77865	153419	251183
CIS	23236	32633	66836	122705
Calf size[1]	**1:** 12% **2:** 75% **3:** 13%	**1:** 12% **2:** 80% **3:** 8%	**1:** 15% **2:** 79% **3:** 6%	**1:** 14% **2:** 79% **3:** 7%
Sex of calf	**M:** 30% **F:** 67%	**M:** 48% **F:** 51%	**M:** 50% **F:** 50%	**M:** 48% **F:** 49%
Age of dam (months)	18 - 48	30 - 62	42 - 202	18 -202

[1]Scored on a categorical scale; 1=small, 2=normal, 3=large

1.3. The estimation of direct and maternal genetic effects

1.3.1. Modelling maternal effects

It is easily conceived that the phenotype of a calf performance trait may be influenced by both the offspring and the mother (dam), commonly referred to as the direct and maternal effect respectively. From the standpoint of the offspring, the influence of a dam can be thought of as an environmental source of variation causing resemblance between offspring, for example through parental care, as described by Falconer (1960). However, it is known that the variance of maternal effects is not completely environmental (Lynch and Walsh, 1997), a simple example of which is the considerable genetic variance of milk production in mammals.

The contribution of the maternal effect to the total phenotype has been modelled in various ways although two main models can be distinguished, that of Willham (1963) and that of Falconer (1964). The difference between Willham's and Falconer's model lies in the base of the model. Willham's model is based upon variance components, which suggests that it models a general and unmeasured maternal performance value which influences the phenotype of the focal individual. Falconer's model is a trait based model which assumes knowledge of the specific characteristics, or traits, that underlie the maternal influence on the phenotype. Falconers' model furthermore models the maternal effect as primarily a source of environmental resemblance between groups; it cannot be easily adapted to take into account a genetic basis of the maternal effect (Falconer and Mackay, 1996). Throughout this thesis we therefore follow Willham's model, described below,

hence there are no prior assumptions made as to what characteristics of the dam underlie the maternal influence on the phenotype of the focal individual.

1.3.1.1. Willham's model

According to Willham's model (1963) the phenotypic value of a calf performance trait can be seen as the result of collaboration between offspring and dam. As such, it is affected by two separate components, the offspring's contribution (direct effect) and the dam's contribution (maternal effect). As said in the previous paragraph, as experienced by the offspring, the maternal contribution is purely environmental. However, differences exist in the genetic ability of dams to provide this environment and these are expressed in their offspring. The phenotype of an individual *i* is modelled by Willham (1963) as,

$$P_i = A_{d,i} + E_{d,i} + A_{m,j} + E_{m,j} \quad [1.1]$$

where P_i is the phenotype of offspring *i*, $A_{d,i}$ is the additive direct genetic effect of offspring *i*, $E_{d,i}$ is the environmental direct effect of offspring *i*, $A_{m,j}$ is the additive maternal genetic effect of dam *j* and $E_{m,j}$ is the environmental maternal effect of dam *j*. This is schematically presented by Figure 1.2 (Willham, 1963).

As Equation 1.1 shows, the maternal effect is a property of dam *j* and is expressed in the phenotype of offspring *i*. Thus, in the life of *i*, the direct additive effect ($A_{d,i}$) is expressed at the start of life while, when *i* is female, the maternal additive effect ($A_{m,i}$) is expressed whenever *i* calves.

The dam therefore makes at least two genetic contributions to the observed phenotype at calving: Firstly, the dam contributes to the observed phenotype by her genetic merit for creating the maternal environment for her offspring, the additive maternal effect; and secondly the dam contributes half of her genes to the offspring

which will be expressed through half of the additive direct effect and half of the additive maternal effect if a female. The phenotypic variance then follows to be

$$\sigma_P^2 = \sigma_{A_D}^2 + \sigma_{A_{DM}} + \sigma_{A_M}^2 + \sigma_{E_D}^2 + \sigma_{E_M}^2 \quad [1.2]$$

assuming no covariance between genetic and environmental effects and direct and maternal environmental effects.

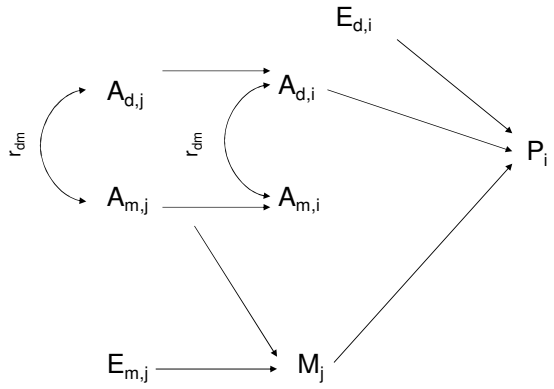


Figure 1.2. Diagram representing the determination of phenotype P where P_i is the phenotype of offspring *i*, $A_{d,i}$ is the additive direct genetic effect of offspring *i,* $A_{m,i}$ is the additive maternal genetic effect of offspring *i* and $E_{d,i}$ is the environmental direct effect of offspring *i*. $A_{d,j}$ is the additive direct genetic effect of dam *j,* $A_{m,j}$ is the additive maternal genetic effect of dam *j* and $E_{m,j}$ is the environmental maternal effect of dam *j*. M*j* is the maternal effect.

1.3.1.2. Direct-maternal genetic covariance

The covariance between an individual's direct and maternal additive component (direct-maternal genetic covariance) represents, using the example of CE, the genetic relationship between the animal's genetic predisposition for ease of being born and ease of giving birth. In the literature, the direct-maternal genetic correlation has been a topic of discussion as it is often estimated to be highly negative, in particular for beef cattle (Koch, 1972; Meyer, 1992). A negative direct-maternal relationship

would suggest that the selection of a sire that is genetically superior for ease of birth will be problematic when, later on, the heifer replacements calve. However, it is well documented that the direct-maternal genetic correlation is sensitive to estimation bias (Koch, 1972; Meyer, 1992; Koerhuis and Thompson, 1997; Bijma et al., 2007). The negatively estimated correlation is therefore often suggested to be a mathematical error due to the fitting of an incorrect model (Koch, 1972; Willham, 1983; Lee and Pollak, 1995; Koerhuis and Thompson, 1997). Several bias theories on the direct-maternal correlation have been reported, ranging from contemporary groups that are not accounted for (Meyer et al., 1992; Lee and Pollak, 1995; Robinson, 1996; Berweger et al., 1999) to ignoring environmental covariances (Falconer, 1965; Koch, 1972; Koerhuis and Thompson 1997; Bijma, 2006; Eaglen, 2009). Occasionally, these bias theories are applied when genetic parameters are estimated, but this is the exception rather than the rule (Koch 1972; Lee and Pollak, 1995; Eaglen and Bijma, 2009).

In this study the bias theory presented by Koch in 1972 will be implemented to prevent and evaluate potential bias in the estimate of the direct-maternal correlation. In the estimation of maternal effects from livestock data, non-additive genetic effects and environmental covariances have by and large been ignored (Meyer, 1992). An example of the latter is the dam-offspring environmental covariance (Koch, 1972), also referred to as the direct-maternal environmental covariance. This covariance ($cov(E_{Di},E_{Mi})$) appears in the phenotypic covariance between the birth record of individual *i* and her (future) calving record, giving birth to individual *k*. Parallel to equation [1.1] the phenotype of individual *k* can be equally described as

$$P_j = A_{D,j} + E_{D,j} + A_{M,k} + E_{M,k} \qquad [1.3]$$

Where P_j is the phenotype of offspring *j*, $A_{d,j}$ is the additive direct genetic effect of offspring *j*, $E_{d,j}$ is the environmental direct effect of offspring *j*, $A_{m,k}$ is the additive maternal genetic effect of dam *k* and $E_{m,k}$ is the environmental maternal effect of dam *k*.

Assuming no covariance between additive and environmental effects, the phenotypic covariance between *i* and *k* then becomes

$$Cov(P_i, P_j) = \frac{1}{2}\sigma^2_{A_D} + 1\frac{1}{4}\sigma_{A_{DM}} + \frac{1}{2}\sigma^2_{A_M} + Cov(E_{m,k}, E_{d,k}) \quad [1.4]$$

The last term in this equation, σ_{Edm}, represents the environmental covariance between the direct effect of *i*, expressed in her own phenotype and the maternal effect of *i*, expressed in the phenotype of her offspring (Koch, 1972; Koerhuis and Thompson, 1997). Generally, this covariance is ignored or assumed negligible and set to zero (Koch, 1972). However, if present, ignoring the covariance can cause bias in the remaining genetic parameters, particularly in the genetic direct-maternal covariance. The effect of disregarding this environmental covariance on the estimation of the direct-maternal genetic covariance was presented first by Koch in 1972 and subsequently further evaluated by several other studies (Meyer, 1992; Koerhuis and Thompson 1997; Eaglen and Bijma, 2009). Although the possibility exists to fit a correlation structure in the residual and avoid this problem, the extra computational complexity is considerable (Eaglen et al., 2009). Therefore, in this thesis, it was chosen to account for this potential bias by removing all individuals appearing both as calf and dam from the data whenever genetic parameters are estimated, such as in Chapter 2 and 3. The possible size of the bias in this dataset was examined by reinstating such animals and repeating the analyses in Chapter 2.

1.3.1.3. Total heritable variance

Additive genetic variances are estimated to gather information about the magnitude of genetic differences that can be used to generate a response to a chosen selection strategy. Under random mating, the additive genetic variance is equivalent to the variance of breeding values of individuals in the population. Equation 1.1 demonstrates that in the case of maternally affected traits, there are two additive genetic variances that can both respond to selection. Analogous to the additive direct genetic variance, the additive maternal genetic variance is equivalent to the variance of maternal breeding values of individuals in the population. The presence of two genetic variances responding to selection raises the question of a 'total' additive variance. Following Bijma et al. (2007) we might express the total breeding value of an individual for a maternally affected trait as the sum of its direct breeding value and its maternal breeding value, which is referred to as the *TBVi*,

$$TBV_i = A_{d,i} + A_{m,i} \quad [1.5]$$

from which the variance follows to be

$$\sigma^2_{TBV} = \sigma^2_{A_D} + 2\sigma_{A_{DM}} + \sigma^2_{A_M} \quad [1.6]$$

In this context, the σ^2_{TBV} represents the total genetic variance available for response to selection, predicted by $R = \tau\rho_M\sigma^2_{TBV}$ where ρ_M is the accuracy of selection (Eaglen and Bijma, 2009). This is distinct from the total heritable variance which has been reported by Willham (1972, 1980), Meyer (1982) and Koch (1972). In these studies, a total heritability by mass selection is constructed. Given current selection strategies in dairy cattle we explore the relevance and practicality of σ^2_{TBV} as described by Bijma et al. (2007) in this thesis.

1.3.2. The estimation of maternal genetic effects

In animal breeding, we are interested in describing the kind and relative amount of genotypic variance for the specific trait examined such that it can be exploited for genetic selection. We estimate this genotypic variance by using a pedigree which allows us to calculate genetic relationships between individuals and subsequently separate the phenotype into a genetic and environmental component. In case of maternally affected traits, there are two genetic variances that need to be quantified, one associated with the direct effects and one associated with the maternal effects. The statistical analysis of maternal traits is therefore far from straightforward. The primary basis of complication constitutes from the way the dam influences the phenotype of her offspring. Namely, the dam contributes in at least two ways to the phenotypic value of her offspring while the sire does so only through his contribution of a sample half of his genes. The confounding of the two contributions of the dam, of the direct and maternal effect, coupled with the possibility of a negative genetic correlation between direct and maternal effects, described before, forms the primary cause of problems in estimating maternal effects. Why this confounding complicates statistical analyses will be described below; this paragraph is mainly adapted from the work of Willham (1980).

1.3.2.1. The problems in estimating direct and maternal effects

Variance component estimation aims to separate sources of variance, additive and environmental, through computing of covariances between relatives, with information on family structure provided by a pedigree (Falconer et al., 1960). A phenotypic value consists of multiple separate components of a trait that are measured jointly and the covariance between the phenotypic values of two relatives

is the sum of the covariances between all separate components (Willham, 1963). Therefore, if there are k components contributing to the phenotype, the covariance between the phenotypic values of two individuals depends on k^2 relationships. There are twice as many components contributing to the phenotype of maternal traits than to that of non-maternal traits (Equation [1.1]), thus many more covariances need to be evaluated in order to calculate genetic and environmental variances. In addition to this large amount of covariances that need to be evaluated, separation of direct and maternal variance components also needs many *types* of collateral relationships. This is due to the considerable overlap in pedigree information for calf and dam from the maternal side, or in other words the maternal effect is confounded with the contribution of the dam to the direct effect. Conventional family structures that are often considered in the estimation of variance components for non-maternal traits, such as full sibs, paternal half sibs and maternal half sibs, are therefore less of a valuable information source for the variance component estimation of maternal traits. Full sibs and maternal half sibs all share the maternal variance and the direct-maternal covariance, thus contribute no information to the separation of these components. Comparison of covariances between paternal half sibs and maternal half sibs test at most the existence of a maternal effect. That is, if the direct-maternal covariance is negative and smaller than the maternal variance. Furthermore, the maternal component which is shared by maternal half sibs will also contain variance due to dominance and common environment. To estimate additive maternal variances free from non-additive genetic variance and environmental variance, maternal genes need to be passed through males. With experimental design, specific relative relationships can be chosen therefore minimising this problem. However in

field data of dairy cattle, types of relative relationships are limited. Maternal effects are further sex limited and occur late in life. This requires that for sire evaluation female relatives are evaluated on the male which lengthens time although this is no different from traits such as milk production. As in traditional variance component estimation, earlier work on the estimation of maternal variances relied on estimating all covariances between relatives separately, equating these to their expectations and solving the resulting system of linear equations The subsequent development of mixed model equations and restricted maximum likelihood led us to the current extended use of animal and sire models in which maternal (co)variance components are estimated as variances due to random effects in the model of analysis (Thompson, 1976; Meyer, 1992). However, while the modern methods of analysis together with the availability of high speed computers and the appropriate software make it easier to estimate genetic parameters due to maternal effects, concern is for these models to make it too easy to ignore the inherent problems of this kind of analyses and to ensure that all parameters fitted can be estimated accurately (Meyer, 1992). Generally, estimates of maternal (co)variance components are subject to large sampling variances, even for a model ignoring dominance effects and family structures providing numerous types of covariances between relatives. Caution with fitting such models, and interpreting results is therefore crucial. Throughout this thesis, this point will be emphasised repeatedly.

1.4. Thesis objectives and outline

The general objective of this thesis is to provide an evaluation of calving traits in UK Holstein-Friesian dairy cattle which generates results that are useful and relevant to the implementation of calving traits in national genetic evaluations such that genetic selection can be used as a tool in the reduction of calving complications.

The thesis has four objectives that are represented by four key questions

1) To what extent do difficult calvings affect the performance of a dairy cattle herd?
2) How can we 'best' evaluate genetic parameters for calving traits?
3) How are calving traits genetically related to other important (selection) traits in dairy cattle breeding?
4) Can the current genomic prediction model for calving ease be improved to increase accuracies of estimated genomic breeding values?

In chronological order, each question is answered in a separate project/chapter.

In Chapter 2 the short and long term gains of improving calving performance are assessed by evaluating the phenotypic effects of a difficult calving on the subsequent performance of both the dam and the calf. The effect of a difficult calving on two rudiments of dairy cattle farming: milk production and fertility, is evaluated by exploring the potential effects of the difficult calving on the subsequent milk production and reproductive performance of affected animals. Having established the significance of calving traits, Chapter 3 then continues with estimating the genetic parameters for calving traits by evaluation of alternative statistical models. A wide range of models are compared on accuracy of estimated genetic parameters and computational burden. Potential bias in the direct-maternal genetic correlation is

explored and gestation length is introduced in this chapter as a highly heritable indicator trait. After having estimated the genetic parameters needed for genetic selection, knowledge of the genetic relationships between calving traits and established selection traits (Hansen et al., 2004; De Maturana et al., 2007; Matilainen et al., 2008) allows the implementation of these traits into national breeding indices. It furthermore provides insight into the potential consequences of genetic selection on calving traits and aids in understanding the role of historical selection decisions in the current state of calving performance in UK dairy cattle. Chapter 4 addresses these issues. Finally, Chapter 5 looks into the future of genetic selection on calving traits. Genomic selection is rapidly winning ground in dairy cattle breeding. Technological developments have made it possible to sequence bulls for an increasing number of Single Nucleotide Polymorphisms (SNPs) by so called high density SNP chips. BLUP models are then adapted to incorporate SNP information which allows the estimation of direct genomic values (DGVs). Theoretically, genomic selection can be of particular benefit to the genetic progress in maternal traits as accuracy is enhanced while the generation interval is not increased. However, genomic models for maternal traits face the same statistical complexities as conventional genetic models, such as BLUP. Chapter 5 looks at the potential of developing a UK genomic model for maternal traits which allows the estimation of DGVs while accounting for complexities regarding maternal effects, such as the direct-maternal genetic covariance.

Finally, Chapter 6 brings all chapters together in a general discussion and conclusion.

CHAPTER 2:

Evaluating the phenotypic effects of a difficult first calving on the reproductive and milk production performance of both dam and calf

Adapted from: Eaglen SA.E, Coffey MP, Woolliams JA, Mrode R, Wall E. 2011. Effect of calving ease on the phenotypic performance of dam and calf in UK Holstein-Friesian heifers. J. Dairy. Sci., 11**:**5413-5423

2.1. Introduction

It is clear that the calving event is a key event for the dairy cow and complications at calving lead to high veterinary and labour costs for the dairy cattle industry. Plus, adding to the importance of an easy calving is the adverse level of pain experienced by the dam (and/or calf) during a difficult calving, which compromises animal welfare. In this Chapter however, we try and find an answer to the question: 'To what extent does a difficult calving effect affect the *performance* of a dairy herd?' If effects on performance are found, this strongly supports the importance of reducing the incidence of difficult calvings in the UK. Numerous studies have currently detected an impairment of performance after a difficult calving, with fertility traits suggested to be most affected e.g. Laster and Gregory, 1973; Tenhagen et al., 2006. This seems highly plausible considering that parturition is a complex process that involves many physiological changes (Chapter 1). Between studies, fertility traits and definition of calving ease scores differ. However, in a number of measures of fertility: days open, calving interval, number of services to conception and days to first service an increase of units following a difficult calving is consistently concluded (Djemali et al., 1987; Simerl et al., 1991; Dematawewa et al., 1997). Alongside fertility traits, production traits are associated with calving ease. Reported 305-day losses in cumulative milk yield after a difficult calving range from 300 kg, (Djemali et al., 1987) to 500-700 kg, (Dematawewa and Berger, 1997) occurring mainly during the first half of lactation (Barkema et al., 1992; Tenhagen et al., 2006; Berry et al., 2007). The effect of calving ease on milk production is typically judged by either the analysis of accumulated milk yield at a number of points in lactation, or the fitting of a function such as the Wilmink exponential equation (Wilmink, 1987;

Berry et al., 2007). However currently, statistical models are capable of fitting flexible curves to longitudinal data using cubic splines (White et al., 1998) which might allow a greater insight into the precise timing and extent of losses in milk production.

Effects of complications in the perinatal period on the development and health of the offspring have been reported in humans (McNeil et al., 1970; Spilsbury et al., 2005; Davis et al., 2006; Yoder, 2008), sheep (Dwyer, 2008), pigs (McNeil et al., 1970), dogs (Silva et al., 2009) rats (Pan et al., 2007; Boksa and Zhang, 2008), and also cattle (Hoffman et al., 1979; Lundborg et al., 2003; Lombard et al., 2007). Yet, studies examining the effects of a difficult birth on the performance of the adult calf are, to our knowledge, rare. Considering that both the dam and the calf undergo the same experience, albeit from different perspectives, it seems likely that complications not only affect the dam, but also affect the subsequent performance of the calf. This then raises the question that the assumed important aspects of calving ease, and hence the gains of genetically improving this trait, may be currently underestimated by the dairy cattle industry.

To answer the research question for this Chapter, the study has two main objectives. Firstly, it aims to estimate the effects of calving ease on reproductive and production performance, using curve fitting with cubic splines for the latter. Secondly, this study aims to estimate the impact of calving ease on not only the subsequent performance of the dam, but equally on the calf, thereby estimating the long-term effect of a difficult birth on the performance of the calf in later life. The study restricts itself to first parity calvings as incidence of difficult calvings is higher in first parity and thus calving ease is of higher importance.

2.2. Materials and Methods

2.2.1. Data editing

From the provided calving ease data as described in Chapter 1, first parity calving records were extracted. In this subset, the age of the dam at calving, parity and breed of dam and sire were checked for inconsistencies and incorrect records were discarded, as were created herd-year contemporary groups with fewer than 2 records. To avoid herds where farmers unrealistically recorded the same calving ease score for most or all contemporary groups of calvings, the standard deviation of calving ease score within herd-year was calculated. Herd-year classes with standard deviations of zero were deleted when this was considered statistically improbable (97.5% confidence interval) given the herd size and calving ease score distribution. The age of dam ranged from 18 to 40 months. Definitions of calving ease scores and details on the harmonisation of scoring scales are given in Chapter 1.

After editing, the first parity calving ease dataset consisted of 43,135 records originating from 2,824 herds. The edited dataset was subsequently matched to fertility data in the lactation following the recorded calving. This was extracted from national databases to create a matched fertility-calving ease dataset for the dams.

All heifer calves were identified from the edited calving ease dataset, specifying the difficulty of their birth, and subsequently matched to the extracted fertility data recorded in their first lactation as heifers. The same procedures were repeated to create a matched production-calving ease dataset for both the dams and the calves. In total, four sets of data were used in this study. Fertility and production data were collected at the same stage of life for both the dam and calf, namely their first

lactation. Data on the calf's first calving as a heifer were not available in sufficient numbers for analyses.

2.2.1.1. Fertility

Matching the calving ease data with the fertility data led to two sets of data with a total of 32,480 and 8,184 records for the dam and calf, originating from 2,486 and 1,410 herds, respectively.

The effect of calving ease on fertility in the subsequent lactation was studied by the analysis of four major fertility traits: calving interval (CI), number of inseminations (NRINS), the binary trait of non-return at 56 days (NR56) (0=failure, 1=success), days to first service (DFS) and body condition score (BCS) as an associated trait. CI was restricted to between 300-600 days and DFS to between 20-200 days. The age of the dam ranged from 19-40 months (first parity heifers, average age of dam equalled 24.3 months), in line with national genetic evaluations. BCS was scored in the field by breed society classifiers in the first half of the lactation (between days 80 and 140 in milk) on a scale from 1 to 9 where 1 = thin and 9 = fat. Scores were then adjusted for classifier by scaling records so the individual standard deviations were equal to the mean standard deviation of all classifiers (Brotherstone, 1994).

2.2.1.2. Production

Merging the calving ease data with individual monthly milk test-day records from national milk recording databases led to two sets of data with a total of 338,665 and 80,679 milk test-day records of 39,473 heifers and 9,507 calves respectively. The mean number of milk yield records per lactation per individual was seven with a maximum number of ten. The effect of calving ease on milk production in the subsequent lactation, for both dam and calf, was studied by the analysis of six

production traits: milk yield (MY), fat yield (FY), fat % (FP), protein yield (PY), protein % (PP) and somatic cell count (SCC).

Milk yield records above 3 standard deviations from the mean milk yield within days in milk (DIM) were deleted and age of dam ranged from 18-40 months.

2.2.2. Statistical analysis

For all models, preliminary least squares analyses using the PROC MIXED option of SAS (SAS institute, 2006) were used to select significant fixed effects to be included. Subsequently random effects were added and analyses were conducted using ASREML v2.0 (Gilmour et al., 2006).

2.2.2.1. Fertility

Fertility traits were analysed using linear regression and Restricted Maximum Likelihood (REML) using ASREML v2.0 (Gilmour et al., 2006) with calving ease fitted as a fixed effect. Least square means of the y-value within each calving ease category were subsequently estimated. The general linear mixed model illustrated by Equation [2.1] was used for analyses of both dams and calves. A generalized linear mixed model fitting a logit link function was used for the analysis of the binary trait of NR56.

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \qquad [2.1]$$

where **y** is a vector of fertility trait records (CI, NRINS(count), NR56, BCS, DFS), **X** and **Z** are known incidence matrices; **b** is a vector of fixed correction factors consisting of sex of calf (only fitted in analyses of the dams), age in months at calving (18,19,…,40), year of calving (1994,1995,…,2009), month of calving (January, February,…, December), calving ease category (1=easy (non-assisted) to

4=veterinary assistance) and data source (A, B). Depending on the trait analysed, fixed covariates added were days in milk (DIM) and days pregnant (DPR). **u** is a vector of the random correction factor of herd-year with **u** ~ N(0, $I\sigma^2_{hy}$); and **e** represents the vector of error terms with **e** ~ N(0, $I\sigma^2_e$).

2.2.2.2. Production

To account for, and estimate, the general shape of the lactation curve for groups of cows in the same calving ease category, production traits were analysed using repeated-measurement analysis. A linear mixed model was fitted, integrating a cubic smoothing spline to the test-day records within each calving ease category. This led to the estimation of four smoothing parameters and sets of curve values, creating four smoothing splines, each representing a lactation curve following a specific calving ease category. The ASREML program fits, by default, 50 equally spaced knot points to the data. To account for the variation of test day measurements at different stages of lactation, residual error classes were fitted. The borders of the residual error classes were based on previous work by Coffey et al. (2002) and Wall et al. (2005) and adjusted to the current data which lead to a number of ten fitted error classes.

The linear mixed model fitted for the analyses of the dams and calves was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Z_s u_s} + \mathbf{e} \qquad [2.2]$$

where **y** is a vector of production trait records (MY, FY, PY, FP, PP, SCC), **X** and **Z** are known incidence matrices linking observations to fixed effects and random correction factors and $\mathbf{Z_s}$ is an incidence matrix containing the spline coefficients for each DIM; **b** is a vector of fixed correction factors consisting of age in months at calving (dams, 18,…,40) or year of birth (calves, 1995,…,2007), year of calving

(1994,…,2009) and data source (A, B). Vector **b** also incorporates the linear part of the fitted cubic splines, calving ease category, DIM (fitted as a covariate) and the interaction term of calving ease category x DIM, **u** is a vector of the random correction factor of herd-test-day (effect specific for all the cows on the same test day within herd) and the permanent environmental effect, with values assumed to be independent and following normal distributions. $\mathbf{u_s}$ is a vector chosen to minimize a roughness penalty, $\alpha \mathbf{u_s R u_s}$, with smoothing parameter α to be estimated by the model, and **R** being a symmetric matrix that is a function of the knot points (White et al., 1998); and **e** represents the vector of error terms with $\mathbf{e} \sim N(0, I\sigma_e^2)$.

2.3. Results

The frequency of calving ease in each of the four datasets is reported in Table 2.1. A lower frequency of difficult births is shown in the calf datasets, which is the result of the merging of datasets. For the merging procedure, only the heifer calves are isolated from the calving ease dataset to match with the adult calf performance datasets. Sex is a significant contributor to calving ease and female calves are known to be born more easily (Meijering, 1983). Discarding the bull calves therefore causes a difference in calving ease frequency between the dam and calf datasets. The calving ease frequencies found in these data are very consistent with the literature, with approximately 70% to 80% non-assisted calvings for primiparous cows (Djemali et al., 1987; Dematawewa et al., 1997; Lombard et al., 2007).

Table 2.1 Frequency distribution of the 4-grade calving ease scale within the production and fertility datasets for cows and calves**.**

	Dataset			
	Fertility		Production	
Category	Cow	Calf	Cow	Calf
1	74.02%	79.70%	74.90%	80.55%
2	22.07%	18.68%	21.39%	18.04%
3	3.19%	1.38%	3.00%	1.18%
4	0.72%	0.23%	0.71%	0.24%

[1]1 = easy (non-assisted), 2 = moderate farmer assistance, 3 = difficult farmer assistance, 4 = very difficult with veterinary assistance.

2.3.1. Effect of calving ease on reproductive performance

Figure 2.1 shows a consistent trend where a decrease in calving ease (categories 2, 3, 4 vs. category 1) is associated with a decrease in subsequent reproductive performance. A summary of significant results for the effect of a difficult calving on the subsequent reproductive performance of the dam is given in Table 2.2. Here, estimated least square means are set to 0 for calving ease category 1, ('easy' (non-assisted)), which then serves as a base of reference for comparison with the other categories, ascending in difficulty.

Dams in need of veterinary assistance (4) at calving required 0.7 more services (s.e.d. = 0.10) to conception, had 8 more days to first service (s.e.d.= 2.3) and experienced a 28 days longer calving interval (s.e.d.= 8.1) compared to non-assisted dams (1). The probability to return to oestrus after 56 days showed a tendency (P-value=0.06) to increase by 11% when veterinary assistance was required, compared to a non-assisted calving. BCS of the dam in the subsequent lactation (scored between days 80 and 140 in milk) was significantly lower following a farmer assisted calving (score 2 and 3), compared to a non-assisted calving. However, a

significant increase in BCS is shown between veterinary and farmer assisted calvings. The increase in BCS when calving ease exceeds category 3 suggests a clear difference in the amount of difficulty and/or assistance experienced between calvings scored within category 3 and category 4.

This study failed to detect an effect of calving ease on the subsequent fertility of the adult calves in their first lactation. From this study, it cannot be concluded that a difficult birth has a long term effect on the reproduction performance of the adult calf in first lactation. Results on both dams and calves are represented in Figure 2.1 This figure excludes the trait of NR56 as, in both dams and calves, a significant effect of calving ease was not found.

Table 2.2 The effects of different degrees of calving ease on the subsequent reproduction performance of the dam expressed as deviations from calving ease score 1. Standard errors of the difference are given in parentheses

	Calving ease category[1,2]			
Trait	1	2	3	4
Calving interval (days)	0.0[a]	4.0[b] (1.37)	6.9[b] (3.47)	28.0[c] (8.05)
Number of services	0.0[a]	0.1[b] (0.02)	0.2[b] (0.04)	0.7[c] (0.10)
Days to 1st service	0.0[a]	1.7[b] (0.51)	3.5[bc] (1.10)	7.8[c] (2.29)
Non-return at 56 days[3]	0.0[a]	-0.04[b] (0.03)	-0.02[ab] (0.04)	-0.11[ab] (0.06)
Body condition score	0.0[a]	-0.06[b] (0.04)	-0.18[b] (0.08)	+0.27[a] (0.16)

[1] $P < 0.05$

[2] 1 = easy (non-assisted), 2 = moderate farmer assistance,
3 = difficult farmer assistance, 4 = very difficult with veterinary assistance

[3] As NR56 is a binary trait, estimates reported for NR56 in this table are probabilities

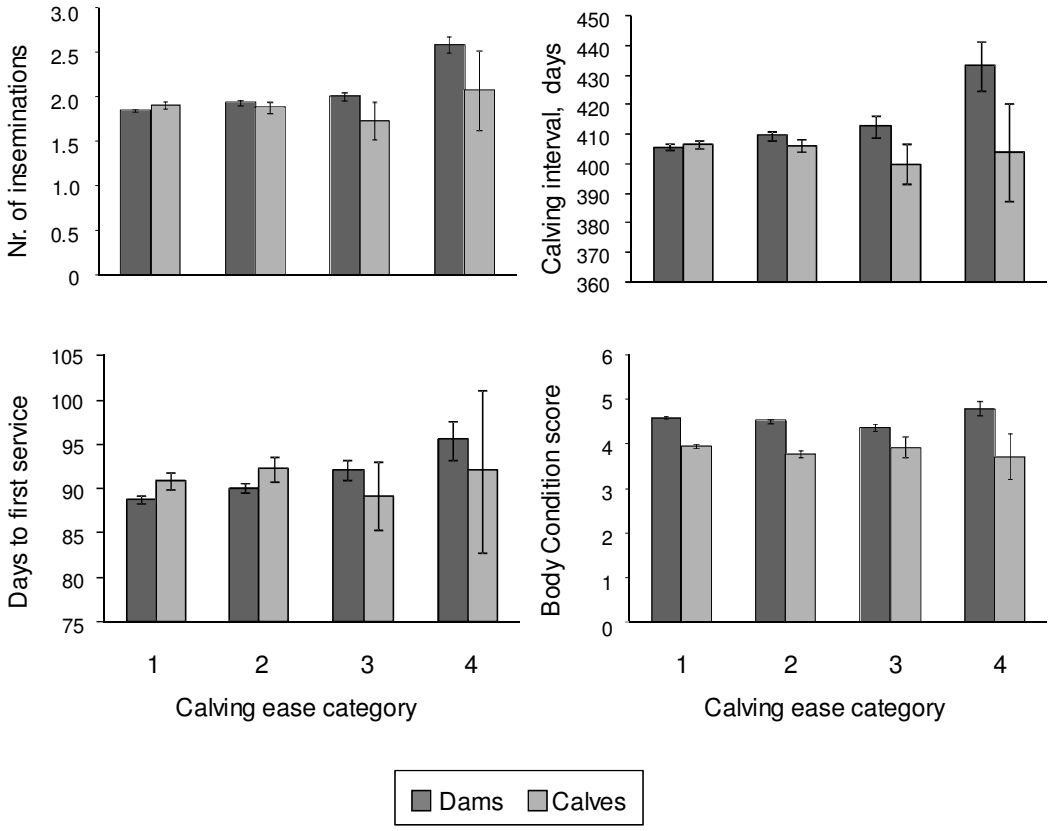


Figure 2.1 The effect of different calving ease categories on the subsequent NRINS, CI, DFS and BCS of the dam and the calf as an adult heifer. Error bars indicate the magnitude of standard errors

2.3.2. Effect of calving ease on production performance

2.3.2.1. Dams

The effect of calving ease on milk, fat and protein production in the subsequent lactation of both the dam and the adult calf is shown by the estimated lactation curves in Figure 2.2. Each estimated curve, within a trait, represents a separate category of calving ease. Veterinary assisted dams show a decrease in their milk production compared to non-assisted dams which is significant between days 10 to 90 in milk, creating a loss in milk yield of approximately 2 kilograms per day. Figure 2.2 illustrates that calving ease does not alter the shape of the lactation curve to a large

extent. The peak of the lactation curve after a veterinary assisted calving is flatter and milk yield decreases more gradually compared to a non-assisted calving. Around day 190 milk yield then meets the level produced by a non-assisted dam. Significant daily loss in milk is therefore estimated to occur solely in the beginning of lactation. The accumulated 305-day milk shows a non significant reduction in milk of 153 ± 102 kg (Table 2.3). The methodology of curve modelling with use of curve parameters produces daily estimates for every day in milk. Therefore, the accumulated 305-day yield presented in Table 2.3 is the sum of all estimated daily milk yields, up to day 305, and not a result of a statistical analysis on the accumulated milk yield to day 305. A reduction in milk yield is logically accompanied by a reduction in fat yield and protein yield, represented by graphs FY (d) and PY (d) in Figure 2.2. A significant reduction in fat and protein percentage was not observed which suggest that milk composition was not altered due to the occurrence of difficulties during calving. This study failed to detect an effect of calving ease on SCC, suggesting no association of difficulty at calving with the occurrence of mastitis infections or other inflammations in the udder. Figure 2.2 shows a consistent trend throughout all the graphs presented. The lactation curve following a veterinary assisted calving is consistently the lowest curve in the graphs while the top curve always represents the lactation following a moderate farmer assisted calving (category 2). The increase in daily milk production levels for a moderate farmer assisted calving compared to non-assisted calving remains significant until the end of lactation, from day 19-304. The accumulated 305-day increase in milk yield is estimated to be 108 kg (± 0.5 kg per day in milk). When quantifying the 305-day accumulated milk loss between a farmer assisted moderate calving and veterinary assisted calving (significant from day 11 to

184 in milk) this is estimated to be 262 ± 104 kg (4% ± 2%), or 1.5 kg per DIM, which approaches the range of 300-700 kg reported in literature (Djemali et al., 1987; Dematawewa and Berger, 1995; Fourichon et al., 1999).

2.3.2.2. Calves

Figure 2.2 presents the effect of different degrees of calving ease on the subsequent milk, fat and protein production of the adult calves and shows very similar trends to the curves representing the production performance of the dams.

Calves delivered by veterinary assistance show a loss in milk production as adult heifers when compared to non-assisted calves. The shape of the lactation curve was not affected by calving ease in the dams. However for the adult calves, a delay in reaching peak milk yield is shown; with veterinary assisted calves reaching peak milk yield approximately a month later than non-assisted calves. The lower level of milk production following a veterinary assisted birth compared to a non-assisted birth is estimated to be significant from day 129 to 261 in milk, (a strong trend (P-value=0.055) was estimated for the first part of lactation). The significant reduction in accumulated 305-day milk yield, presented in Table 2.4, is estimated at 703 ± 251 kg (9% ± 3%) for a veterinary assisted calf compared to a non-assisted calf. Similar to the dams, higher milk yield levels are shown by calves delivered with moderate farmer assistance compared to no assistance at all. This benefit is expressed by an estimated increase in accumulated 305-day milk yield of 153 kg, or 0.5 kg a day, and was significant throughout the lactation. Please note that the calf dataset was small (9,507 calves) compared to the dam dataset and therefore the number of animals, especially in categories 3 and 4 was low. Therefore, estimated standard errors are relatively large.

Table 2.3 The effects of different degrees of calving ease on the subsequent production of milk (MY), fat (FY) and protein (PY) of the dam. Standard errors are given in parentheses.

		Calving ease category[1,2]							
Trait	DIM	1		2		3		4	
MY, kg									
	100	26.11	(0.29)	26.52	(0.29)	26.21	(0.32)	25.62	(0.41)
	200	23.13	(0.29)	23.54	(0.29)	23.40	(0.31)	23.00	(0.41)
	300	18.54	(0.29)	18.93	(0.30)	18.77	(0.35)	18.49	(0.48)
	Cum.[3]	7218.73[ac]	(104)	7326.91[a]	(105)	7249.22[a]	(108)	7064.85[c]	(119)
FY, kg									
	100	0.98	(0.01)	1.00	(0.01)	0.99	(0.01)	0.96	(0.02)
	200	0.92	(0.01)	0.94	(0.01)	0.93	(0.01)	0.91	(0.02)
	300	0.80	(0.01)	0.82	(0.01)	0.80	(0.02)	0.80	(0.02)
	Cum.	283.75[a]	(17)	288.95[a]	(17)	285.43[a]	(17)	277.56[a]	(17)
PY, kg									
	100	0.82	(0.01)	0.83	(0.01)	0.82	(0.01)	0.80	(0.01)
	200	0.77	(0.01)	0.78	(0.01)	0.78	(0.01)	0.77	(0.01)
	300	0.66	(0.01)	0.67	(0.01)	0.67	(0.01)	0.66	(0.02)
	Cum.	234.31[a]	(15)	236.76[a]	(16)	233.72[a]	(15)	228.56[a]	(16)

[1] $P < 0.05$

[2] 1 = easy (non-assisted), 2 = moderate farmer assistance, 3 = difficult farmer assistance, 4 = very difficult with veterinary assistance.

[3] Cumulative

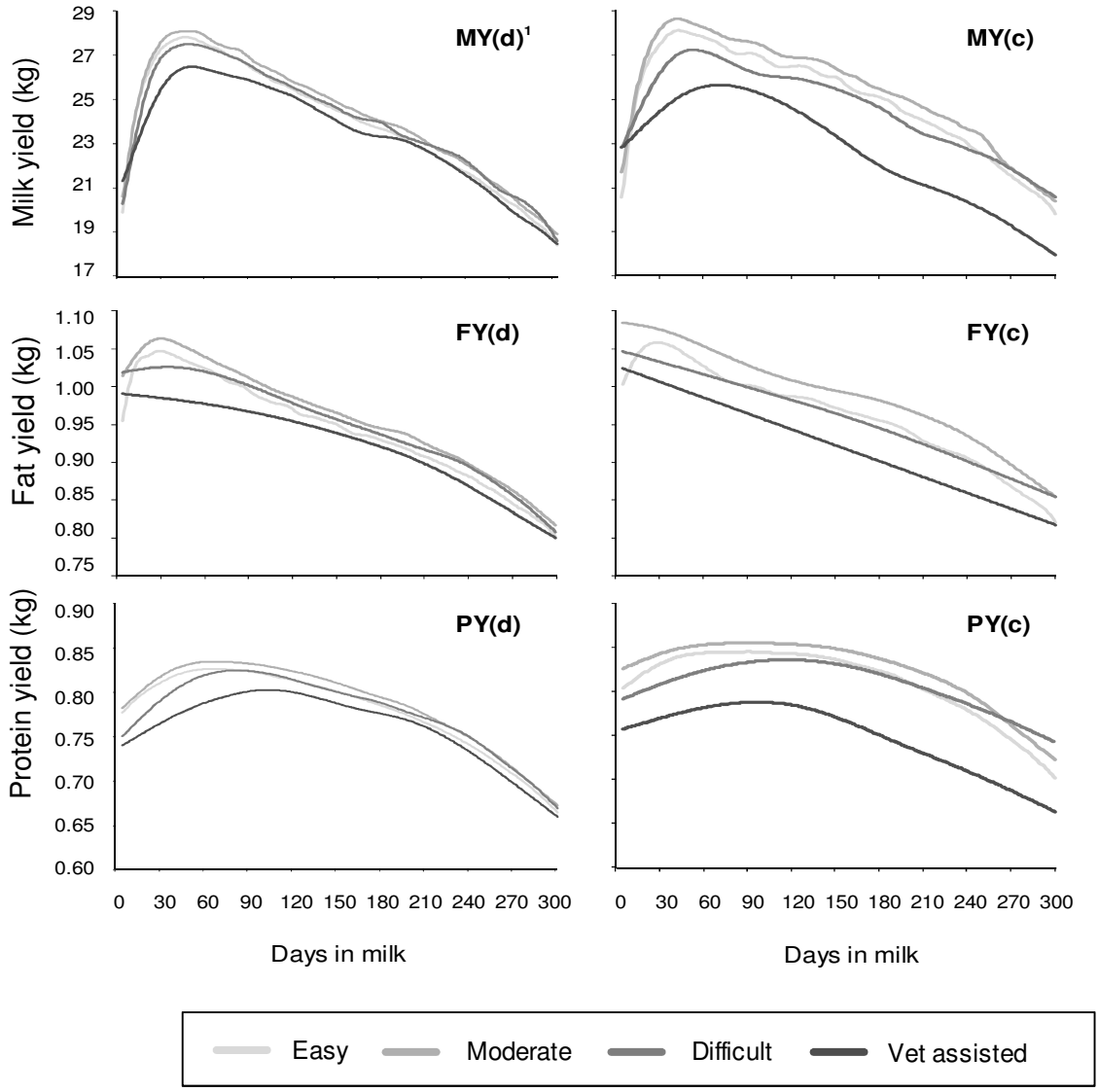
Table 2.4 The effects of different degrees of calving ease on the subsequent production of milk (MY), fat (FY) and protein (PY) of the calf as an adult heifer. Standard errors are given in parentheses.

		Calving ease category[1,2]							
Trait	DIM	1		2		3		4	
MY, kg									
	100	26.77	(0.15)	27.27	(0.19)	26.10	(0.53)	25.16	(1.16)
	200	24.35	(0.15)	24.95	(0.19)	23.88	(0.53)	21.22	(1.16)
	300	19.82	(0.18)	20.45	(0.23)	20.67	(0.72)	17.40	(1.83)
	Cum.[3]	7502.74[ab]	(59)	7655.81[a]	(93)	7384.01[b]	(134)	6798.89[c]	(245)
FY, kg									
	100	0.99	(0.01)	1.01	(0.01)	0.97	(0.02)	0.99	(0.05)
	200	0.94	(0.01)	0.97	(0.01)	0.94	(0.02)	0.87	(0.05)
	300	0.82	(0.01)	0.85	(0.01)	0.85	(0.03)	0.82	(0.08)
	Cum.	289.03[a]	(12)	297.32[a]	(17)	287.97[a]	(17)	276.78[a]	(19)
PY, kg									
	100	0.84	(0.01)	0.85	(0.01)	0.83	(0.02)	0.80	(0.04)
	200	0.81	(0.01)	0.82	(0.01)	0.81	(0.02)	0.73	(0.04)
	300	0.70	(0.01)	0.72	(0.01)	0.74	(0.02)	0.63	(0.06)
	Cum.	243.55[a]	(14)	247.87[a]	(16)	242.95[a]	(16)	224.93[a]	(17)

[1] $P < 0.05$

[2] 1 = easy (non-assisted), 2 = moderate farmer assistance, 3 = difficult farmer assistance, 4 = very difficult with veterinary assistance

[3] Cumulative



[1] Here, 'd' refers to the graphs representing the performance of the dams, and 'c' refers to the performance of the calves as grown-up heifers

Figure 2.2 The effect of different degrees of calving ease on the subsequent milk yield, fat yield and protein yield of both the dams and calves as grown-up heifers

2.4. Discussion

This study has found substantial effects of calving ease on the subsequent reproductive performance of the dam but failed to detect any effects on the reproductive performance of the adult calf in first lactation. Lactation curves estimated by using curve fitting show significant effects of calving ease on the milk production of the dam as well as the calf. To our knowledge, this is the first study to determine detrimental effects of a difficult birth on performance of the calf later in life, using national data. No effect of calving ease on SCC was found, in accordance with Berry et al. (2007). Comparing the estimated effects of calving ease found in this study with estimates in the literature is difficult (Fourinchon et al., 1999). This is because scoring procedures vary widely among studies by using different numbers and definitions of categories. Even though the highest category generally refers to veterinary assisted calvings and the lowest to calving with 'no difficulties', categories that lie between are not consistent in definitions. Furthermore the rearrangement of recorded scores into assisted and non-assisted calvings, preceding statistical analysis, is not uncommon (Berry et al., 2007). As in the results, emphasis in the discussion therefore lies in differences between the outer classes of the 4-grade scale (1 vs. 4), where score 4 (veterinary assistance) includes caesareans.

2.4.1. Effect of calving ease on reproductive performance

While many studies have reported detrimental effects of calving ease on all the fertility traits analysed in this study (Thompson et al., 1983; Erb et al., 1985; Djemali et al., 1987; Simerl et al., 1991; Dematawewa et al., 1997); a few studies did not find significant results (Laster et al., 1973; Tenhagen et al., 2006). However, in these studies, sample sizes were small and it was acknowledged that severe difficulty at

calving decreases conception rate to AI and the likelihood of conceiving within 200 days in milk. The estimated effects of a difficult calving on the subsequent reproduction performance are of similar magnitude to estimates reported in the literature. Reported estimates range from 0.2 to 0.4 more services for NRINS, from 14 to 45 days longer CI or days open, from 4 to 8 days for DFS, and a drop in probability of NR56 by 0.14 to 0.25 for a veterinary assisted calving compared to a non-assisted calving (Meijering, 1983; Thompson et al., 1983; Mangurkar et al., 1984; Erb et al., 1985; Djemali et al., 1987; Simerl et al., 1991; Dematawewa et al., 1997).

Good fertility in dairy cows can be defined as the establishment of pregnancy at the desired time (Pryce et al., 2004). As conception is the end result of a chain of events, failure to establish pregnancy can be the result of malfunction at any link in this chain (Garnsworthy et al., 2008). However, the consistency in reported results on DFS suggests that after a difficult calving, problems start early in this chain with a struggle to return to normal cyclicity. The anoestrus following a difficult calving is a prolonged luteal phase due to the lack of luteal regression (Peter et al., 2009). A stressful event, such as a difficult calving, can act as an acute stressor affecting the hypothalamic function in such a way that this results in abnormal ovarian function. This then delays or prohibits the surge of luteinizing hormone (LH), which is necessary for ovulation (Dobson et al., 2001). Such mechanisms are consistent with the results of Zhang et al. in 1999, who reports delays in the decline of progesterone concentration found in heifers after having had a difficult calving.

After calving, high energy requirements for milk production force the dam into a period of negative energy balance. To offset energy required in excess of ingested

energy, body tissue is catabolised and consequently body condition score decreases. Additional stress due to a difficult parturition might cause a greater negative energy balance, due to reduced appetite (Ingvartsen et al., 2003). A reduction in BCS experienced after a difficult calving, as found in this study, does not seem surprising, and is supported by other reports in dairy (Berry et al., 2007) and beef cattle (Drennan et al., 2006). A very high body condition score is frequently associated with a higher risk of experiencing a difficult calving (Meijering, 1983; Mee, 2008). In this context, the greater than expected BCS found in this study to be associated with a veterinary calving may be an indirect consequence of high BCS at parturition. Such inference is acceptable since BCS in this study was scored in the first part of the lactation. Higher BCS found in veterinary assisted dams compared to non-assisted dams could also be associated with additional results of this study showing a lower milk production following veterinary assistance. However, further studies will be required to fully explore the consequences a difficult calving on BCS postpartum.

2.4.2. Effect of calving ease on production performance

2.4.2.1. Dams

This study shows that by use of curve fitting with cubic splines, lactation curves can be estimated, showing the milk, fat and protein yields per day in milk, after calvings of different ease. With this method, 'gaps' are avoided between estimations of accumulated milk yields at specific days in milk. By comparing the estimated lactation curves, it was possible to accurately determine when losses in milk yield occur and around which day differences lose their statistical significance. It was shown that losses in milk yield after a veterinary assisted calving vs. a non-assisted calving are significant up to day 90 in milk. After day 90 in milk, differences in milk

yields gradually decrease and become negligible around day 190 in milk. These results thereby explain why the effect of calving ease was only reported significant in the first stage of lactation by studies analyzing accumulated 30, 60, 90, 120 and 240 day in milk yields (Thompson et al., 1983; Tenhagen et al., 1999 and Berry et al., 2007). By having fitted cubic splines, daily milk yields and milk production trends can be accurately compared between calving ease categories. This allows determination of no evidence for compensatory milk production, something which could not have been concluded from analyses on accumulated milk yields at specific days in milk. The lack of statistical significance for later accumulated yields is seen to be due the additional variance and dilution of the effect.

The estimated lactation curves in this study show a moderate benefit in milk yield when farmer assistance was provided at a calving of moderate difficulty (category 2). Biologically, it appears illogical that a decrease in calving ease would be related to an increase in milk production. Therefore, it seems sensible to consider this phenomenon as being an artefact of industry recorded data. In that context, the estimated benefit in milk production can be supported by various hypotheses, or most likely, a combination of these. Firstly, the presence of a farmer at parturition might indicate preferential treatment. This could be in the form of additional care provided to the animals by nutrition, or an isolated location, that is beneficial to their milk production. The animals involved in a farmer assisted calving may also be of higher value, with associated expectations. For example, animals of comparatively high genetic merit for yield in the herd are more readily offered assistance. Secondly, it is inevitable that a considerable number of calvings are unobserved by the farmer. Therefore witnessing a healthy cow and calf may encourage the farmer to assume the

calving went as desired and score it as a calving of category 1. However the exact amount of difficulty experienced by the dam and calf remains unknown, thereby biasing the category defined as 'easy'. This bias, if one assumes that difficult calvings will reduce yield to some degree, would then lead to a depression of the yield in the 'easy' class.

In this study, the occurrence of stillbirths or retained placenta has not been corrected for. Both retained placenta and stillbirth have been associated with loss in milk yield (Rowlands and Lucey, 1986; Erb, 1987; Fourichon et al., 1999; Berry et al., 2007) and calving ease, stillbirth and retained placenta have been reported to occur as a complex. This lack of independence and confounding (Thompson et al., 1983; Rajala et al., 1998) raises the possibility that the observed detrimental effect of calving ease on milk production is to some degree indirectly resulting from the impacts of retained placenta and stillbirth (Fourichon et al., 1999). Correction for stillbirth and retained placenta estimates the impact of calving ease conditional on the absence of these events. This may potentially be of value for subsequent studies, but differences will exist between these estimates and the true expected loss conditional on observing a given score. In the end, the loss of milk due to a difficult calving is of economic importance to the farmer, whether this was caused solely by difficulty at calving or in combination with related complications. Therefore presentation of the full effect of calving ease is of primary importance to the dairy cattle industry. The effect of a difficult calving on the milk production of the dam presented in this study is purely phenotypic, further research is needed to estimate the genetic contribution to this relationship.

2.4.2.2. Calves

The study described in this Chapter is one of the first to try and estimate the effect of a difficult birth on the subsequent milk production of the adult calf. The establishment of a significant long term effect of a difficult birth on future production performance is therefore a new finding of interest in dairy cattle. However, that does not mean that this finding is entirely surprising. Studies in other species have shown that complications during the perinatal period are associated with numerous problems throughout life including low vigour, reduction in growth, susceptibly to disease, mortality, reduction in development of the foetal central nervous system, abnormal temperament, and impaired learning ability (McNeil et al., 1970; Dwyer, 2003; Lundborg et al., 2003; Spilsbury et al., 2005; Davis et al., 2006; Yoder, 2006; Lombard et al., 2007; Pan et al., 2007; Boksa and Zhang, 2008; Silva et al., 2009).

At present we can merely speculate about possible causes and mechanisms underlying the negative effects of a difficult birth on the subsequent milk production of the adult calf. Further research is needed to identify the mechanisms that underlie this phenomenon. Literature on the concept of 'developmental programming' provides hypotheses which could help in the understanding of the specific relationship addressed in this study. The concept of 'developmental programming' has only recently been embraced by animal agriculture, as being influential for animal growth, development and well-being, either through *in utero* mechanisms or epigenetic processes (Hill et al., 2010). Therefore, studies linking prenatal and early postnatal experiences, primarily malnutrition and maternal stress, to animal performance in livestock are fairly recent (Weaver et al., 2004; Ford et al., 2007; Du et al., 2010; Blair et al., 2010). Long-term changes of gene expression in the

hypothalamus-pituitary-adrenal axis and mammary gland of several animal species, both by long-term chronic events and short-term acute events, have recently been reported in reviews by Kapoor et al. (2006) and Rijnkels et al. (2010). Thereby, these reviews give conceptual support to the findings in this study. Hypotheses such as 'developmental programming' however need to be considered in the light of future research considering genetic correlations of calving ease with type and production. At this moment, hypothesising is not a priority. Now, most important is to acknowledge that a difficult birth can have long term effects on the performance of the adult calf and recognize that this problem needs to be addressed. The results of this study are confirmed by results of Heinrichs et al. (2011), where the effect of a difficult birth on subsequent milk production was estimated in an experimental setting (795 calves). Here, it was found that as difficulty at delivery increased by 1 unit, first lactation 305-day actual milk production was decreased by 284.6 kg. This supports the equivalent estimate in this study, where the reduction in milk production between easy versus veterinary assisted births equalled 703 ± 251 kg.

High expectations of the industry rest on the performance of a dairy cow, especially concerning milk production. Therefore, all events that potentially prohibit the animal from showing her full genetic potential should be considered, even if these events are not identifiable in surroundings of the cow in her productive life. A difficult calving evidentially shows to have both short and long term effects for dam and calf, thereby strengthening the importance of calving ease as a selection trait

2.5. Conclusions

Results of this study clearly show that difficulty during first calving has detrimental effects on the performance of the dairy herd by affecting performance of both the dam and adult calf. Reproductive performance of the dam in first lactation worsened following a difficult calving, with increased days to first service, number of services needed to conceive and a prolonged calving interval. A significant loss in milk production of a veterinary assisted dam was shown in the first part of lactation, compared to a non-assisted dam. In the case of moderate difficulty at calving, the presence of a farmer seemed to have a beneficial effect on the milk production of both the dam and calf. Redefinition of the calving ease categories to allow inclusion of a category defined as 'not-observed' should therefore be considered.

The establishment of a long term effect of a difficult birth on the milk production of the calf in later life is a new finding of interest. The general assumption that difficulties during birth do not affect subsequent calf performance, due to the time interval between birth and lactation is therefore incorrect. The physiological effects, or causes underlying a difficult birth, appear to be long lived. This problem needs to be addressed and further studies must be undertaken.

CHAPTER 3:

The evaluation of different models to estimate genetic parameters of calving traits in UK Holstein-Friesian dairy cattle.

Adapted from: Eaglen SAE, Coffey MP, Woolliams JA and Wall E 2012**.** Evaluating alternate models to estimate genetic parameters of calving traits in United Kingdom Holstein-Friesian dairy cattle. Genetics Selection Evolution, 44:23

3.1. Introduction

Now that the importance of reducing the incidence of calving complications in the UK has been strongly supported by Chapter 2, we proceed to estimate the genetic parameters needed if genetic selection is to play a role in achieving this goal. Hence, in this Chapter we try and find an answer to the question: How can we 'best' estimate genetic parameters for calving traits in the UK?

As explained in Chapter 1, dairy cattle breeders have shown an increasing interest in selection for functional traits in recent years (Mark, 2004) and gradually the focus of selection is shifting from traits that increase profit towards traits that reduce costs (De Maturana et al., 2007). As important non-production traits, there has also been increasing interest for the selection on calving traits, yet the estimation of genetic parameters, and subsequently breeding values, for these traits is not straightforward. Firstly, calving ease (CE) and stillbirth (SB) are phenotypes that are generally scored on categorical or binary scales which make them sensitive to subjectivity (Chapter 1), especially CE (Dekkers, 1994). Furthermore, heritabilities of these traits are suggested to be low (Meijering, 1984) and thus much data is needed to obtain sufficiently accurate estimates that have an impact on selection indices. But above all, calving traits are maternal traits and variance component estimation is thereby complicated (Chapter 1) The statistical model fitted for calving traits should allow the separation and estimation of both direct and maternal effects but there is no consensus on which is the most accurate model to achieve this objective. Various statistical models have been reported throughout the years, each aimed at improving one aspect of their predictive ability. Consequently, many different statistical models are used in routine genetic evaluations to estimate genetic parameters for calving

traits (Interbull, 2012), while for production traits there is a greater consensus across countries (Mark, 2004). For CE, statistical models range from sire-maternal grandsire (sire-mgs) models to animal models in univariate or multi-trait form that either allow a direct-maternal genetic covariance or fix this covariance to zero (Interbull, 2012). Overall, statistical models can account for direct and maternal effects in two ways i.e. animal models that fit calf and dam effects directly and sire-mgs models that fit direct and maternal effects through the sire of the calf and dam, respectively (Interbull, 2012). Each of these then has a family of implementation depending on how traits are defined and modelled e.g. univariately or multi-trait, which leads to the divergence in models seen today. The genetic covariance between direct and maternal effects plays a key role in the interpretation of estimated genetic parameters and the prediction of response to selection, but is sensitive to estimation bias (Chapter 1). Estimation of the direct-maternal covariance and remaining genetic components is said to be further improved by using a multi-trait model instead of a univariate model (Hansen et al., 2004; De Maturana et al., 2009). Since CE and SB are highly correlated and show low heritabilities, it has been suggested that a multi-trait model that incorporates a highly heritable and correlated indicator trait such as birth weight, calf size and/or gestation length (GL), would lead to a more optimal analysis (Hansen et al., 2004; De Maturana et al., 2009; Matilanen et al., 2009). In addition to models incorporating indicator traits, it has also been proposed that the extension of univariate models to a multi-trait model between parities would be useful because of the potential genetic distinctiveness of calving traits in first and later parities. This implies that models fitting first and later parities as correlated

traits are theoretically more correct than models that fit parity as a non-genetic effect (Steinbock et al., 2003; De Maturana et al., 2008; Wiggans et al., 2008).

However, given the high standard errors of the estimated maternal variances and direct-maternal covariances, it appears that statistical models used to analyse calving traits can still benefit from optimization. Previous studies on the estimation of genetic parameters for calving traits have compared models. However, in most cases, studies limit themselves to single comparisons, such as univariate versus multi-trait models within either a sire or animal model framework (Wiggans et al., 2008; De Maturana et al., 2009).

The study described in this Chapter had the objective to estimate the genetic parameters of calving traits for United Kingdom (UK) Holstein-Friesian cattle with a range of present-day statistical models for national genetic evaluations of calving traits. A comparison was made between sire-mgs versus animal models and univariate versus multi-trait models between traits and parities.

GL was added to the multi-trait model to study any benefits of this indicator trait to the predictive ability of the model. Specific attention was given to the potential bias of the sensitive genetic correlation between direct and maternal effects and, lastly, a 'total heritable variance' for calving traits was estimated, combining direct and maternal variance components as described in Chapter 1. Its practical use for calving traits is discussed.

3.2. Material and Methods

3.2.1. Data description

For this study, first and later parity records were extracted separately from the data described in Chapter 1. The datasets contained 43,135 and 330,753 records respectively, spanning the years 1995 to 2009. The data were checked for inconsistencies in parity, breed, calving date and age at calving. Incorrect records were discarded, as were contemporary groups with fewer than two records (herd, herd-year, sire and maternal grandsire). Age at calving was restricted to 18-48 months for heifers and 30-70 months for cows. The standard deviation of CE score within herd-year was calculated and corrected for as described in Chapter 2.

Sex of stillborn calves was not recorded by one of the data sources. As sex has been shown to have a considerable effect on SB (Meijering, 1984) data from this specific data source was deleted for the univariate and bivariate between-parity analyses on SB. For all univariate analyses on CE and GL, the data from this source for a stillborn calf was set as missing but the remaining data obtained by the specific data source was used. The final dataset consisted of 30,640 first parity records originating from 2,098 herds representing 2,012 (service) sires and 4,783 maternal grandsires (MGS). The accompanying pedigree consisted of ~ 200,000 individuals and was 5 generations deep. Since the later parity dataset created computational problems when fitting the animal model, it was reduced by only retaining records that were of 2nd and 3rd parity and had values for each of the three traits (prior to edits on SB data described earlier). Furthermore, the thresholds for the minimum size of herd-year and sire contemporary groups were increased to 7 and 5 records, respectively. Finally, the final later parity dataset consisted of 54,744 records, originating from 2,108 herds,

1,918 sires and 5,886 maternal grandsires, with an accompanying pedigree of ~ 290,000 individuals that was 4 generations deep.

CE and SB scores were as explained in Chapter 1 where detailed information on the recording system and transformation of CE scores can also be found. Frequency distributions per data source within edited datasets, GL means, SB frequencies and other descriptive statistics of the data are given in Table 3.1.

Table 3.1 Descriptive statistics of the data

		Dataset		
Variable		First parity	Later parities	Across parities
Number of records		30,640	54,744	83,053
Number of dams		30,640	51,658	79,967
Number of dams with own birth record[1]		2,411	10,899	13,310
Number of sires		2,012	1,918	2,827
Number of maternal grandsires		4,783	5,886	8,291
Female calves		67.12%	46.08%	54.6%
Male calves		32.88%	53.92%	46.4%
CE, frequency[2,3]	1	71.67%	83.12%	79.03%
	2	24.33%	14.99%	18.54%
	3	3.33%	1.51%	2.20%
	4	0.67%	0.38%	0.50%
GL (days), mean ± s.e.[3]		280.69 ± 4.97	281.35 ± 4.89	281.17 ± 4.93
SB, frequency[3]		11.6%	4.3%	6.0%

[1]The total number of records reported (30,640) excludes this subset of records; [2]1 = easy (non-assisted), 2 = moderate assistance (veterinarian called as precaution), 3 = difficult, 4 = very difficult with veterinary assistance; [3]CE = calving ease, GL = gestation length, SB = stillbirth, s.e. = standard error

3.2.2. Statistical analyses

3.2.2.1. Gestation length

Multi trait models allow for the evaluation of genetic relationships between traits, and account for these relationships in the resulting estimated genetic parameters. In addition, multi trait models facilitate the usage of multiple sources of information which can benefit the predictive ability of the statistical model compared to a single trait or univariate model, depending on the correlation between sources. It has been found that CE and SB are phenotypically and genetically related to other traits that are involved in the calving process. Birth weight and gestation length are most associated with calving traits and calf size is often mentioned as a third optional indicator trait (Janss and Foulley, 1983; Varona et al., 1999; Hansen et al., 2004). Because of the close biological relationships between calving related traits and the generally low heritabilities of CE and SB it has been suggested that a multi trait model, incorporating an (higher heritable) indicator as a correlated trait, might be preferred over a single trait model (Hagger, 1989; Janss and Foulley 1993; Groen et al., 1998; Lee et al., 2002; McClintock et al. 2003; Hansen et al., 2004). In view of the data provided, it was decided to evaluate the benefit of multi trait models by fitting gestation length (GL) as a correlated indicator trait. In addition to theoretical benefits, GL is linked to CI and is therefore potentially an economically relevant trait for farm management. Hence, estimated genetic parameters of this trait may also be of interest to the dairy cattle industry. Therefore all analyses, including univariate analyses, were also conducted for the trait of GL. GL has been reported to be highly heritable and moderately correlated to calving performance traits (Groen et al., 1998; Hansen et al., 2004; Norman et al., 2009). A non-linear phenotypic relationship

between GL with both CE and SB has been reported (McGuirk et al., 1998; Hansen et al., 2004). Here, an extremely short gestation is associated with a higher frequency of SB and difficult calvings due to under development of the fetus while a long gestation is linked to a difficult calving and SB due to the relatively oversized calf. It is therefore possible that genetic associations of GL with CE and SB are non-linear (Philipsson, 1976; McGuirk et al., 1998; Hansen et al., 2004) which was tested prior to analyses and will be further discussed in the Results section. Finally, the phenotype of GL is, like CE and SB, also affected by a direct and a maternal effect. Hence, both the fetus and dam contribute genetically and environmentally to the observed length of gestation

3.2.2.2. Statistical models

In all cases, optional fixed effects and potential interaction effects were tested for significance in SAS V9.1 ($P < 0.05$) (SAS v9.1, 2009) and then the variance components were calculated using REML, with ASREML version 3.0 (Gilmour et al., 2009). Sex by parity and sex by age interaction effects were not significant. Prior to using multi-trait models involving GL, the relationship of GL with CE and SB was examined according to Hansen et al. (2004) to ensure that the use of traditional bivariate models was appropriate given their assumption of linearity.

Furthermore, the limitations of analysing categorical traits, such as CE and SB, with linear models are well known as model assumptions are violated due to the fact that values of categorical data are bounded within certain limits e.g. 0 to 1 or 1 to 4. Therefore, generalized linear mixed models (GLMM) such as threshold models can be more appropriate for the analysis of categorical traits since scores are transformed by the model into values on an underlying continuous liability scale. This study

aimed to evaluate statistical models with the ultimate goal of implementation in national genetic evaluations of CE, SB and GL. Although threshold models are implemented in routine national genetic evaluations in France and the United States of America (Ducrocq, 2000; Wiggans et al., 2003), in the UK and most other countries, calving traits are evaluated with a linear model. Therefore, we chose to evaluate several modelling possibilities within linear rather than threshold models. In the discussion section of this paper, we will elaborate further on this choice. In this study, all models will follow Willham's model (1963) as described in Chapter 1.

3.2.2.2.1. Univariate animal and sire-mgs models

To study the difference between animal and sire-mgs models, first parity data were analysed by linear univariate models. Direct and maternal genetic effects were incorporated by fitting genetic effects for calf and dam for the animal model and sire and maternal grandsire for the sire-mgs model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_d\mathbf{a}_d + \mathbf{Z}_m\mathbf{a}_m + \mathbf{Z}_{hy}\mathbf{h}_{hy} + \mathbf{e} \quad . \qquad [3.1]$$

In equation 3.1, $\mathbf{y}$ is a vector representing the observations for CE, SB or GL; $\mathbf{X}$, $\mathbf{Z}_d$, $\mathbf{Z}_m$ and $\mathbf{Z}_{hy}$ are known incidence matrices for non-genetic, direct and maternal genetic and herd-year effects, respectively; $\mathbf{b}$ is a vector of non-genetic effects, $\mathbf{a}_d$ is a vector of the random direct additive-genetic effects of the calf (sire), $\mathbf{a}_m$ is a vector of the random maternal additive- genetic effects of the dam (maternal grandsire), $\mathbf{h}_{hy}$ is a vector of random herd-year effects and $\mathbf{e}$ is a vector of residuals. Vectors $\mathbf{a}_d$ and $\mathbf{a}_m$ were assumed to follow a multivariate normal distribution, with MVN(0, $\mathbf{G} = \mathbf{G_0} \otimes \mathbf{A}$) where, $\mathbf{G_0}$ was a 2 x 2 direct-maternal (sire-mgs) variance-covariance matrix, $\otimes$ is the Kronecker product of matrices, and $\mathbf{A}$ was the relationship matrix. $\mathbf{e}$ was assumed to be MVN(0, $\mathbf{I}\ \sigma^2_e$), where $\mathbf{I}$ denotes the identity matrix and σ^2_e the residual

variance. Non-genetic effects in the models included sex of the calf, herd, sire breed (only for GL), year and month of calving, the interaction of year and month of calving; age of the dam (months) treated as a covariate and the interaction of herd and year of calving treated as a random factor. Sire-mgs models yield sire and maternal grandsire (co)variances ($\sigma^2_{sire}, \sigma^2_{mgs}, \sigma_{sire,mgs}$) which were subsequently transformed algebraically into direct and maternal (co)variances ($\sigma^2_{A_D}, \sigma^2_{A_M}, \sigma_{A_{DM}}$) according to

$$\sigma^2_{A_D} = 4\sigma^2_{sire}$$

$$\sigma_{A_{DM}} = 4\sigma_{sire,mgs} - 2\sigma^2_{sire} \qquad [3.2]$$

$$\sigma^2_{A_M} = 4\sigma^2_{mgs} + \sigma^2_{sire} - 4\sigma_{sire,mgs}$$

3.2.2.2.2. Bivariate models between traits

Bivariate animal models were fitted pairwise among CE, SB and GL, separately for first and later parity data:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & 0\\ 0 & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{D\_1} & 0\\ 0 & \mathbf{Z}_{D\_2}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{D\_1}\\ \mathbf{a}_{D\_2}\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{M\_1} & 0\\ 0 & \mathbf{Z}_{M\_2}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{M\_1}\\ \mathbf{a}_{M\_2}\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_{hy} & 0\\ 0 & \mathbf{Z}_{hy}\end{bmatrix}\begin{bmatrix}\mathbf{h}_{hy\_1}\\ \mathbf{h}_{hy\_2}\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} \qquad [3.3]$$

In this model, vectors and incidence matrices correspond to those in the univariate animal model (Equation 3.1) and subscripts 1 and 2 denote traits. Non-genetic effects for later parities were the same as for univariate first-parity models, with the addition of an interaction between age of dam and parity treated as a fixed factor, and a random permanent environmental effect ($\mathbf{Z}_{pe}\mathbf{pe}_{pe}$). The covariance matrix of the genetic terms equalled, $\mathbf{G} = \mathbf{G_0} \otimes \mathbf{A}$ where $\mathbf{G_0}$ was a 4 x 4 symmetrical direct-maternal variance-covariance matrix

$$\text{Var}\begin{bmatrix}\mathbf{a}_{D\_1}\\ \mathbf{a}_{D\_2}\\ \mathbf{a}_{M\_1}\\ \mathbf{a}_{M\_2}\end{bmatrix}=\begin{bmatrix}\sigma^2_{A_{D\_1}} & & & \\ \sigma_{A_{D\_1,2}} & \sigma^2_{A_{D\_2}} & & \\ \sigma_{A_{D\_1,M\_1}} & \sigma_{A_{D\_2,M\_1}} & \sigma^2_{A_{M\_1}} & \\ \sigma_{A_{D\_1,M\_2}} & \sigma_{A_{D\_2,M\_2}} & \sigma_{A_{M\_1,2}} & \sigma^2_{A_{M\_2}}\end{bmatrix}\otimes\mathbf{A}\,. \qquad [3.4]$$

Residuals, **e**, and permanent environmental effects, $\mathbf{pe}_{\text{pe}}$, were assumed to be MVN(0, $\mathbf{R}_{\text{e}}\sigma^2_e$), and MVN(0, $\mathbf{R}_{\text{pe}}\sigma^2_{pe}$), where $\mathbf{R}_{\text{e}}$ and $\mathbf{R}_{\text{pe}}$ denote the residual and permanent environmental 2 x 2 variance covariance matrices and σ^2_e and σ^2_{pe} were the residual variance and permanent environmental variance.

3.2.2.2.3 Bivariate models between parities

To study the genetic correlation between calving traits in first and later parities, bivariate sire-mgs models were fitted with first and later parities (2nd and 3rd parities combined) treated as correlated traits. The model was described by equation 3.3, where $\mathbf{y}_{\text{i}}$ is now a vector representing the observations for each trait in first (y_1) and later parities (y_2). Random genetic effects were fitted for the sire and maternal grandsire. The fixed and random non-genetic effects were the same as in the univariate animal model. Estimates of sire and maternal grandsire variances were transformed into direct and maternal effects according to equation 3.2.

Direct and maternal heritabilities (h^2_d and h^2_m) were estimated by:

$$h^2_D = \sigma^2_{A_D}/(\sigma^2_{A_D} + \sigma_{A_{DM}} + \sigma^2_{A_M} + \sigma^2_E) \qquad [3.5]$$

and

$$h^2_M = \sigma^2_{A_M}/(\sigma^2_{A_D} + \sigma_{A_{DM}} + \sigma^2_{A_M} + \sigma^2_E) \qquad [3.6]$$

where $\sigma^2_{A_D}$and $\sigma^2_{A_M}$ are the direct and maternal additive genetic variances, $\sigma_{A_{DM}}$ is the additive direct maternal covariance and σ^2_E is the environmental variance. To allow

easy comparison with other studies, herd-year variances and permanent environmental variances were not included in the phenotypic variance but can be found in Tables 3.4 and 3.5. The heritabilities and genetic direct-maternal correlations were estimated more than once by the several bivariate models and these were pooled in meta- analyses according to Corbin et al. (2010).

3.2.2.3 Direct-maternal genetic covariance

A negative direct-maternal relationship would be worrying for the dairy cattle industry since it suggests that selecting a sire that is genetically superior for ease of birth may later cause a problem when its daughters calve. Koch (1972) showed that, when ignored or assumed to be zero, a direct-maternal environmental covariance ($cov(E_{d,i,} E_{m,i})$) can cause bias in the estimated genetic parameters. Although it is possible to fit a correlation structure in the residual to avoid this problem, computational complexity is then substantially increased. Therefore, in this study, we chose to avoid this potential bias by removing from the data all individuals that appeared as both calf and dam. Residuals of these specific records would otherwise be correlated (Eaglen et al., 2009). Then to evaluate the bias, animals were reintroduced and the analyses were repeated. Throughout the paper, animal model 1 (A1) represents the animal model which was used to analyse the reduced data, whereas animal model 2 (A2) represents the animal model used to analyse the total data.

3.2.2.4 Total heritable variance

Additive genetic variances are estimated to evaluate the genetic differences between animals that can be used to generate a response to a chosen selection strategy. In

Chapter 1, it was demonstrated that in the case of maternally affected traits, there are two additive genetic variances that can respond to selection. Analogous to the additive direct genetic variance, the additive maternal genetic variance is equivalent to the variance of maternal breeding values of individuals in the population, under random mating. The presence of two genetic variances responding to selection raises the question of a 'total' additive variance. According to Bijma et al. (2007), the total breeding value of an individual for a maternally affected trait can be expressed as the sum of its direct breeding value ($A_{D,i}$) and its maternal breeding value ($A_{M,i}$), which is referred to as the *TBVi* and is further described in Chapters 1 and 6. In this study, we estimated and explored σ^2_{TBV} as described by Bijma et al. (2007).

3.3. Results and Discussion

Table 3.1 presents the descriptive statistics of the data. It shows that in the UK, approximately 20% of the calvings required assistance of some sort. The incidence of calving assistance was higher in first than in later-parity calvings, which agrees with the general consensus that calving complications are of more concern in heifers than in cows (Meijering, 1984). Moreover, severe calving difficulty was experienced by approximately 4% and 2% of heifers and cows respectively. These are in line with international prevalence of calving difficulty in the Holstein breed (Mee, 2007) although comparison is not straightforward since the scoring system of CE allows for a large variety of score definitions (Meijering, 1984). The incidence of SB in first and later parities (Table 3.1) agrees with incidences reported by Hansen et al. (2004) and Jamrozik et al. (2005). Table 3.1 also shows that there were fewer males than females in the first-parity dataset, which could indicate a bias in data recording due

to the difference in value between a bull and a heifer calf in dairy cattle. Since the calving of bull calves is known to be more difficult (Eaglen et al., 2009), it is possible that CE is under-reported. However, all studies using field records for CE data in dairy cattle will likely suffer from the same problem. The frequencies of female and male calves were more equal in later parities.

Given the amount of results obtained in this study, it was decided to separate the biological findings (genetic parameters), in Tables 3.2 to 3.7, from the findings on the model comparisons. To aid in the comparison of different models, accuracies of predicted transmitting abilities (PTAs) for 25 randomly selected young and older sires were calculated by their prediction error variances (PEV) where PEV=$(1-r^2)$ $\sigma^2_{A_D}$ (Table 3.8). The PEV are provided in Table 3.9. Throughout the study, the default model fitted was A1. When results of other models are discussed, this is indicated.

3.3.1. Genetic parameters

3.3.1.1. Heritabilities

Tables 3.2 and 3.3 show the estimates of heritabilities and genetic correlations among traits obtained from bivariate animal models in first and later parities and Table 3.6 presents parameter estimates obtained by between-parity models for each trait. Therefore, results for later parities in Table 3.6 account for selection based on first parity, whereas results in Table 3.3 do not. All heritabilities estimated for CE, SB and GL were within the range of previously published estimates of these traits in dairy cattle (Steinbock et al., 2003; Eaglen et al., 2009; Norman et al., 2009). Heritabilities of CE were low (direct: 12% first parity and 3% later parities; maternal:

5% first parity and 2% later parities) and the direct heritability was approximately twice as large as the maternal heritability. GL appeared moderately heritable, with the direct heritability (57% first parity and 41% later parities) being considerably larger than the maternal heritability (7% first parity and 7% later parities). This supports the view that the genetic variation of this trait lies primarily in the triggering of parturition by the foetus (Azzam et al., 1987; Maitilanen et al., 2009; Norman et al., 2009) rather than in the maternal response to this trigger. All heritabilities were larger in first parity than in later parities, as reported elsewhere in the literature (Meijering, 1984; Steinbock et al., 2003). This supports the general assumption that the variation in calving performance is larger in heifers than in cows (Clutter et al., 1989; Wiggans et al., 2008). In addition, heritability estimates are frequency dependent when applying linear models to categorical traits. Both direct and maternal heritabilities for SB were low, irrespectively of parity, with the direct heritability ranging from 1.8% to 2.0% (not significant in first parity) and the maternal heritability ranging from 2.0% to 3.2%. These estimates agree with values from the literature, which range from 1.6% to 10% for direct heritability and from 2.0% to 13% for maternal heritability (Azzam et al., 1987; Luo et al., 2002; Jamrozik et al., 2005; Heringstad et al., 2007; Matilanen et al., 2009; Norman et al., 2009)

3.3.1.2. Direct and maternal genetic correlations

3.3.1.2.1. Within traits and within parities

The estimated genetic direct-maternal correlations for CE and GL presented in Tables 3.2, 3.3 and 3.6 were low to moderate (-0.52 to -0.22). For GL, the direct-maternal correlations were not significantly different from zero. For CE, a significant genetic relationship between the direct and maternal effects in first parity (-0.53) was detected. This negative direct-maternal correlation suggests that animals with a lower genetic risk of being born with difficulties are genetically prone to have more difficulty at first calving. Numerous studies confirm a negative genetic relationship between the direct and maternal effect of CE (Thompson et al., 1980; Carnier et al., 2000; Lee et al., 2002), although positive correlations also appear in the literature (Steinbock et al., 2003). The negative genetic correlation between direct and maternal effects of CE implies that dairy farmers need to base selection decisions on both the direct and the maternal PTA of a sire for CE in first parity, to avoid long-term negative consequences. An optimum index value for genetic merit in CE is therefore preferable, as discussed later.

Due to very low heritabilities and very high standard errors, the estimated direct-maternal genetic correlation of SB, obtained by the different models, were not informative. Studies estimating this covariance in large datasets (> 400,000) report correlations close to zero (Carnier et al., 2000; Steinbock et al., 2003; Hansen et al., 2004), although with considerable standard errors. To date, there is no clear evidence to recommend a change from the common practice of assuming this covariance as equal to zero.

3.3.1.2.2. Between traits

Table 3.2 shows the estimated genetic correlations between the direct and maternal effects of CE, SB and GL in first parity heifers obtained from bivariate analyses. Table 3.3 shows the estimates of the same models for later parity cows (parity 2 and 3). In general, CE and SB were strongly genetically correlated, whereas the relationships of GL with CE and SB were weak to moderate. Both the direct and maternal correlations between CE and SB were positive and high in first parity (0.84; 0.85), and positive and moderate in later parities (0.37; 0.67). This suggests that both difficult birth and difficult calving are genetically associated with a higher frequency of direct and maternal stillbirth respectively, regardless of parity. The findings for the UK dataset thereby support the consensus of a strong genetic relationship between CE and SB (Thompson et al., 1980; Carnier et al., 2000; Lee et al., 2002; Hansen et al., 2004; Heringstad et al., 2007; Cervantes et al., 2010). In this study, correlations of CE and SB were not significantly different from 1. However, Hansen et al. (2004) and Cervantes et al. (2010) provide evidence of genetic differences for these traits, with estimates of similar magnitude to those from this study, but with smaller standard errors. Furthermore, a simple meta-analysis (Corbin et al., 2010) pooling estimates from this study and four other studies (Thompson et al., 1983; Hansen et al., 2004; De Maturana et al., 2009; Cervantes et al., 2010) resulted in direct and maternal genetic correlations between CE and SB of 0.79 ± 0.02 and 0.65 ± 0.03, respectively, which suggests a degree of genetic difference of these traits.

The genetic correlations between GL and the calving traits differed between parities (Table 3.2 and 3.3). A moderate positive genetic correlation (0.65) was found between maternal GL and maternal SB in first parity. This suggests that an individual

with a longer than average gestation period is genetically more likely to give birth to a stillborn calf in first parity and *vice versa*. Genetic correlations between GL and SB in later parities were not significant (Table 3.3). A direct genetic relationship between GL and CE was detected, but only in later parities. No maternal relationship was detected in later parities. The direct effect of GL was found to be moderately correlated to the direct effect of CE. This positive correlation (0.50) between direct CE and direct GL suggests that a calf that gestates longer before birth to a multiparous dam is genetically prone to a difficult birth and *vice versa*. Similar positive correlations between direct GL and direct CE are reported in beef cattle (Cervantes et al., 2010), Danish Holstein cattle (Hansen et al., 2004) and UK Holstein cattle (McGuirk et al., 1998), and support the findings from the UK dataset here. However, in this study, the genetic correlation between maternal GL and maternal CE was non-significant, although this relationship is generally reported to be low to moderate (Hansen et al., 2004; De Maturana et al., 2009).

All relationships between direct effects of one trait and maternal effects of the other trait (and *vice versa*) were non-significant, except for the genetic correlation between direct SB and maternal CE in first parity, which was high and positive. This specific relationship is difficult to estimate at the animal level and the high estimate may be due to the inaccuracy of the SB variance components. In general, studies in the literature report non-significant genetic correlations between the genetic direct effects and the genetic maternal effects between traits (Hansen et al., 2004; De Maturana et al., 2008; Cervantes et al., 2010; Johanson et al., 2011).

Table 3.2 Estimated genetic parameters[1] for calving ease, gestation length and stillbirth from first parity bivariate animal models

	Trait[2]					
Trait[2]	h^2	DSB	DGL	MCE	MSB	MGL
DCE	0.12 (0.02)*	0.84 (0.18)*	0.18 (0.10)	-0.53 (0.13)*	0.28 (0.23)	0.02 (0.19)
DSB	0.02 (0.01)		-0.06 (0.27)	0.97 (0.23)*	0.37 (0.56)	-0.15 (0.14)
DGL	0.57 (0.05)*			0.09 (0.14)	-0.30 (0.23)	-0.23 (0.11)
MCE	0.05 (0.01)*				0.85 (0.13)*	-0.15 (0.12)
MSB	0.03 (0.01)*					0.65 (0.32)*
MGL	0.07 (0.02)*					

*P < 0.05; [1]Heritabilities and genetic correlations [2]DCE = direct calving ease, DSB = direct stillbirth, DGL = direct gestation length, MCE = maternal calving ease, MSB = maternal stillbirth, MGL = maternal gestation length; standard errors are indicated in brackets

Table 3.3 Estimated genetic parameters[1] for calving ease, gestation length and stillbirth from later parities bivariate animal models

		Trait[2]				
Trait[2]	h^2	DSB	DGL	MCE	MSB	MGL
DCE	0.03 (0.01)*	0.37 (0.17)*	0.50 (0.08)*	-0.27 (0.22)	-0.16 (0.22)	-0.22 (0.16)
DSB	0.02 (0.00)*		-0.08 (0.12)	-0.22 (0.31)	-0.88 (0.20)*	-0.24 (0.24)
DGL	0.41 (0.02)*			0.04 (0.14)	-0.30 (0.19)	0.01 (0.08)
MCE	0.02 (0.01)				0.67 (0.19)*	0.13 (0.18)
MSB	0.02 (0.01)*					-0.06 (0.25)
MGL	0.07 (0.01)*					

*P < 0.05; [1]Heritabilities and genetic correlations [2]DCE = direct calving ease, DSB = direct stillbirth, DGL = direct gestation length, MCE = maternal calving ease, MSB = maternal stillbirth, MGL = maternal gestation length; standard errors are indicated in brackets

Table 3.4 Herd-year variances estimated with univariate and bivariate first parity models for calving ease, gestation length and stillbirth

		Parameter
	Trait[1] and model	σ^2_{hy}
Univariate first parity	CE	
	sire-mgs model[2]	0.037 (0.003)
	A1[2]	0.038 (0.003)
	A2[2]	0.037 (0.003)
	SB	
	sire-mgs model[2]	0.002 (0.0001)
	A1[2]	0.003 (0.0001)
	A2[2]	0.002 (0.0001)
	GL	
	sire-mgs model[2]	0.706 (0.13)
	A1[2]	0.677 (0.14)
	A2[2]	0.685 (0.13)
Bivariate first parity	CE	
	SB	0.034 (0.003)
	GL	0.034 (0.003)
	SB	
	CE	0.002 (0.001)
	GL	0.003 (0.001)
	GL	
	CE	0.673 (0.14)
	SB	0.686 (0.14)

[1]CE=calving ease, GL=gestation length, SB=stillbirth [2]sire-mgs=sire-maternal grandsire model, A1 = animal model 1 excludes animals recorded at birth and calving, A2 = animal model includes all records; standard errors are indicated in brackets

Table 3.5 Herd-year and permanent environmental variances estimated with bivariate later parity animal models for calving ease, gestation length and stillbirth

			Parameter	
	Trait[1] and model		σ^2_{hy}	σ^2_{pe}
Bivariate later parity	CE			
		SB	0.019 (0.001)	0.017 (0.006)
		GL	0.019 (0.001)	0.017 (0.006)
	SB			
		CE	0.005 (0.0003)	0.0003 (0.0006)
		GL	0.005 (0.0003)	0.0003 (0.0006)
	GL			
		CE	0.508 (0.06)	1.167 (0.33)
		SB	0.508 (0.06)	1.167 (0.33)

[1]CE=calving ease, GL=gestation length, SB=stillbirth; standard errors are indicated in brackets

3.3.1.2.3. Between parities within traits

Table 3.6 presents the genetic parameters estimated by the bivariate sire-mgs models that treat first and later parity records as correlated traits. Estimated genetic correlations between first and later parities were 0.80 ± 0.12 for direct CE and 0.84 ± 0.15 for maternal CE. These estimates are similar to those estimates obtained by the threshold model reported by Wiggans et al. (2008) but slightly higher than those reported in general (Steinbock et al., 2003; Heringstad et al., 2007; Cervantes et al., 2010). Among the studies estimating genetic correlations of CE between parities, there is general agreement that both direct and maternal CE are genetically distinct traits in first and later parities, which suggests that both ease of birth and ease of calving represent a different trait in heifers and in cows (Steinbock et al., 2003; Wiggans et al., 2008; Cervantes et al., 2010). However, the standard errors reported here are too large to infer genetic differences between first and later parities from this study alone.

Direct and maternal GL are rarely considered separately in studies that estimate between-parity correlations. Table 3.6 shows that different between-parity genetic correlations were estimated for direct GL and maternal GL. This emphasizes the fact that direct and maternal GL are separate traits, and thus must be analysed and interpreted with this in mind. For direct GL, the estimated correlation between first and later parities was near unity (0.96 ± 0.02) but the same correlation for maternal GL was lower (0.82 ± 0.13). However, in this case too, the standard error is too large to conclude that maternal GL is a distinct trait in first and later parities. Other studies on larger datasets show a correlation that is high but nevertheless significantly different from 1 (Van Pelt et al., 2009; Norman et al., 2010) which implies that maternally, the gestation length of a heifer and a cow are genetically distinct traits.

When fitting a between-parity sire-mgs model for SB, results were difficult to obtain. Other analyses, using univariate and bivariate models, already showed the difficulty of obtaining an accurate estimate of the direct-maternal genetic correlation for SB within parities. With the between-parity model, the likelihood surface was practically flat which hampered convergence to sensible estimates.

Table 3.6 Genetic parameters[1] (s.e.) for CE, SB and GL across parities and within traits

			Direct		Maternal	
Trait[2]			First	Later	First	Later
CE	Direct	First	0.11 (0.022)			
		Later	0.80 (0.119)	0.03 (0.006)		
	Maternal	First	-0.47 (0.130)	-0.12 (0.174)	0.08 (0.019)	
		Later	-0.40 (0.215)	-0.28 (0.195)	0.84 (0.150)	0.02 (0.007)
SB	Direct	First	0.016 (0.01)			
		Later	-	0.017 (0.01)		
	Maternal	First	0.57 (0.47)	-	0.024 (0.01)	
		Later	-	-0.88 (0.20)	-	0.011 (0.01)
GL	Direct	First	0.30 (0.024)			
		Later	0.96 (0.022)	0.38 (0.017)		
	Maternal	First	0.01 (0.119)	0.13 (0.109)	0.05 (0.013)	
		Later	-0.22 (0.101)	-0.04 (0.088)	0.82 (0.125)	0.05 (0.011)

[1] Heritabilities (diagonals) and genetic correlations (off-diagonals) [2]CE = calving ease, GL = gestation length, SB = stillbirth; standard errors are indicated in brackets

3.3.1.3. Total heritable variance

The total heritable variance gives a holistic measure of the genetic variance affecting calving and accounts for both the maternal and direct sources of variance. Although some estimates in this study were inaccurate (in particular the direct-maternal genetic covariance for SB), the estimates of σ^2_{TBV} presented in Table 3.7 show how the maternal variance and direct-maternal genetic covariance contribute to the total genetic variance. Focusing on animal model A2, the total variance was smaller than the direct variance for CE and GL by 26% and 3%, respectively, although these differences were not significant. For SB, the very large and positive direct-maternal genetic covariance, in combination with the small direct variance, caused σ^2_{TBV} to be ~ 400% larger than the additive direct variance.

When a farmer makes a selection decision based on a maternally affected trait, population mean performances change in response to both its direct and maternal breeding value. The TBV_i as described by Bijma et al. (2007) is suggested to represent the total additive value of an individual. However, it does not represent the impact of that individual on the population mean since this impact will depend on the time period and the frequency of expression of the direct and maternal effects in the population within that period. Gene flow methodology (Wolfová et al., 2004; Wall et al., 2011) shows that contributions of the direct and maternal effects to genetic change in calving traits depend on several factors which determine how often the maternal effect is expressed, e.g. how many calvings, how many calves are kept as replacement heifers and the breeding system (pure breeding or crossbreeding). Therefore, while theoretically TBV_i and σ^2_{TBV} show the importance of considering maternal effects and their interrelationship with direct effects, practically, an index

value that is not the simple sum and represents the total impact of an individual would be useful to farmers. This would be in addition to the separate direct and maternal PTA that are already provided.

3.3.2. Model comparison

In this section, animal models are compared to sire-mgs models, and univariate models to bivariate models. Furthermore, the benefit in treating first and later-parity calvings as correlated traits in a bivariate between-parity model is discussed. A potential bias due to an environmental direct-maternal covariance is also evaluated. All models that are discussed are linear models. Several studies have explored the advantages of threshold models over linear models for the analysis of calving traits (Phocas et al., 2003; Lee, 2002) given that according to the categorical nature of the traits, threshold models should theoretically be superior, as explained by Gianola (1982). Findings show that computational requirements are greater for threshold compared to linear models and Monte Carlo methods are needed to obtain the most reliable parameter estimates. However, software that can estimate variances without relying on Monte Carlo simulation methods, e.g. through the use of approximations to maximum likelihood in complex GLMM is available but limited (McCulloch, 1997). For calving traits, comparisons between linear and threshold models have shown very high correlations between PTA, meaning that the ranking of sires is not greatly influenced by the use of a linear model (Clutter et al., 1989; Weller et al., 1989; Phocas et al., 2003). Threshold models have been shown to take specific interactions into account which can potentially be problematic for linear models (Quaas et al., 1988; Manfredi et al., 1991).

3.3.2.1. Animal model versus sire-mgs model

Table 3.7 contains the results of the univariate analyses on first parity data and compares animal model A1 with the sire-mgs model, since neither of these two models are expected to show bias due to the ignored environmental direct-maternal covariances discussed in the Methods, unlike animal model A2.

Table 3.7 shows that, between traits, direct heritabilities and phenotypic variances when estimated by A1 and sire-mgs models were very similar but the residual variances were consistently larger for sire-mgs models compared to both A1 and A2 models. The residual variance of a sire-mgs model contains the default environmental variance plus a Mendelian sampling term and the remaining unexplained additive variance terms from dams totalling $\frac{9}{16}\sigma^2_{A_D} + \frac{3}{4}\sigma^2_{A_M} + \frac{3}{4}\sigma_{A_{DM}}$.

Accuracies of PTA for young and older sires are presented in Table 3.8. Comparison of the sire-mgs model with A1 and A2 models shows that there was only a small loss in accuracy when fitting the sire-mgs model. In some cases, mainly for older sires for which more progeny information is available, there was an increase in accuracy of PTA when the sire-mgs model was fitted as opposed to the animal model. This is probably due to the slightly higher heritabilities that were estimated by the sire-mgs model. The computation time required with univariate animal models was 10 times greater than with univariate sire-mgs models. Furthermore, when increasing the model complexity, animal models failed to converge, whereas sire-mgs models were robust. The between-parity model in this study was an example where animal models failed, whereas sire-mgs models performed well. Advantages in computation time and versatility of the sire-mgs model therefore compensate well for the slight loss in accuracy of any resulting estimates.

3.3.2.1.1. Potential bias in the direct-maternal genetic correlation

Table 3.7 also shows the estimated genetic direct-maternal correlations within traits for first parity data, when applying two univariate animal models. As described earlier, part of the data corresponding to specific dam-offspring pairs was deleted from the dataset (7.8%) to remove a potential environmental direct-maternal covariance. In Table 3.7, animal model A1 represents the analysis of the edited data, whereas A2 represents the analysis of the complete data. Comparison of the results for A1 and A2 models shows that deleting records on dam-offspring pairs had only a small and non-significant impact on direct-maternal genetic correlations. The observed change implies that the environmental direct-maternal covariance was negative and small in this dataset. Since estimates of the direct-maternal genetic correlation do not differ significantly, the magnitude of the environmental covariance in this dataset is likely to be negligible and changes observed could be due to chance alone.

Table 3.7 Variance components and genetic parameters estimated for calving ease, gestation length and stillbirth from first parity univariate animal and sire-mgs models

[1]Trait [2]Model	Variance components and genetic parameters[3]							
	σ^2_P	$\sigma^2_{A_D}$	$\sigma^2_{A_M}$	σ^2_{TBV}	σ^2_e	h^2_D	h^2_M	r_{DM}
[1]CE								
sire-mgs[2]	0.464 (0.01)	0.050 (0.01)	0.024 (0.01)	0.048 (0.01)	0.443 (0.01)	0.108 (0.02)	0.051 (0.02)	-0.373 (0.15)
A1[2]	0.464 (0.01)	0.055 (0.01)	0.022 (0.01)	0.041 (0.01)	0.404 (0.01)	0.119 (0.02)	0.048 (0.01)	-0.523 (0.13)
A2[2]	0.462 (0.01)	0.054 (0.01)	0.022 (0.01)	0.046 (0.01)	0.401 (0.01)	0.117 (0.02)	0.033 (0.01)	-0.444 (0.13)
[1]SB								
sire-mgs[2]	0.096 (0.001)	0.002 (0.001)	0.002 (0.001)	0.006 (0.001)	0.094 (0.001)	0.016 (0.01)	0.024 (0.01)	0.567 (0.47)
A1[2]	0.097 (0.001)	0.002 (0.001)	0.002 (0.001)	0.006 (0.002)	0.092 (0.001)	0.017 (0.01)	0.018 (0.01)	0.704 (0.75)
A2[2]	0.095 (0.001)	0.002 (0.001)	0.002 (0.001)	0.006 (0.002)	0.090 (0.001)	0.019 (0.01)	0.022 (0.01)	0.623 (0.62)
[1]GL								
sire-mgs[2]	24.30 (0.51)	12.06 (1.31)	1.99 (0.50)	12.35 (1.25)	18.95 (0.20)	0.496 (0.05)	0.081 (0.02)	-0.172 (0.12)
A1[2]	23.50 (0.42)	13.22 (1.41)	1.65 (0.45)	12.85 (1.19)	9.64 (0.85)	0.563 (0.05)	0.070 (0.02)	-0.216 (0.11)
A2[2]	23.32 (0.37)	11.66 (1.20)	1.67 (0.41)	11.86 (0.96)	10.73 (0.71)	0.499 (0.05)	0.072 (0.02)	-0.166 (0.11)

[1]CE = calving ease, GL = gestation length, SB = stillbirth; [2]sire-mgs=sire-maternal grandsire model, A1 = animal model 1 excludes animals recorded at birth and calving, A2 = animal model includes all records; [3] σ^2_P = phenotypic variance, $\sigma^2_{A_D}$ = additive genetic direct variance; $\sigma^2_{A_M}$ = additive genetic maternal variance; σ^2_{TBV}= variance of total breeding values; σ^2_e = environmental variance; h^2_D = direct heritability; h^2_M= maternal heritability; r_{dm} = genetic direct-maternal correlation; standard errors are indicated in brackets

3.3.2.2. Univariate versus bivariate models

One of the important points when using GL as an indicator trait for the analyses of calving traits is its potential non-linear relationship with CE and SB. The relationship of GL with both SB and CE was clearly non-linear on a phenotypic scale (Figure 3.1, first parity). However, a visual assessment of plotted estimated breeding values (EBVs) obtained from univariate first parity animal models showed that relationships were not better approximated by a quadratic relationship (quadratic regression coefficients $P > 0.05$) than by a linear relationship. Figure 3.2 and 3.3 show this for 150 sires with > 25 progeny. Thus, it was concluded that quadratic relationships between GL, CE and SB were not detected and that, for this study and under the assumption that relationships of higher polynomial degree would be unlikely, the use of GL as indicator trait in linear bivariate models was justified.

Table 3.8 demonstrates that, for calving traits, bivariate models are slightly superior to univariate traits. In particular, the maternal variance of low heritable traits (CE and SB) benefitted from including a correlated trait in the model. Accuracies of direct PTA also showed a slight improvement from bivariate analysis, in particular for the low heritable SB trait. Estimates obtained for SB heritabilities with the univariate and bivariate models (Tables 3.7 and 3.2) demonstrate that these models provided nearly identical estimated direct variances, although the maternal variance showed a small but significantly higher estimate with bivariate analyses. Strong genetic correlations were found between CE and SB, SB and GL, and CE and GL, which are likely to explain the increase in accuracy of PTA obtained by the bivariate model compared to the univariate model. The maternal variance of the indicator trait, GL, also benefitted from the bivariate model compared to the univariate model, although the accuracy of

the maternal PTA of GL was slightly decreased with the bivariate model. Genetic direct-maternal correlations for CE and GL showed little change between univariate and bivariate models, while the estimate of this correlation for SB showed considerably more change but is too imprecise to be interpreted.

3.3.2.3. Inclusion of later parities

Calving traits in first and later parities were highly correlated, which results in a considerably greater predictive ability of PTA for all traits when later parity information is added as a correlated trait to the model (Table 3.8). Accuracies increased, for both direct and maternal PTA of CE and GL, when compared to the univariate model.

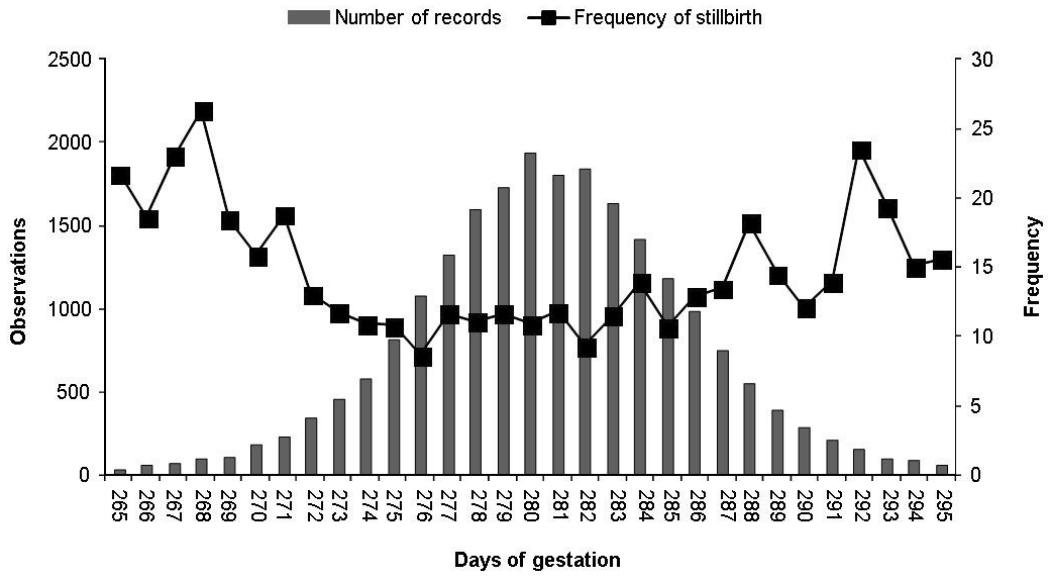


Figure 3.1 Phenotypic relationship between gestation length and stillbirth

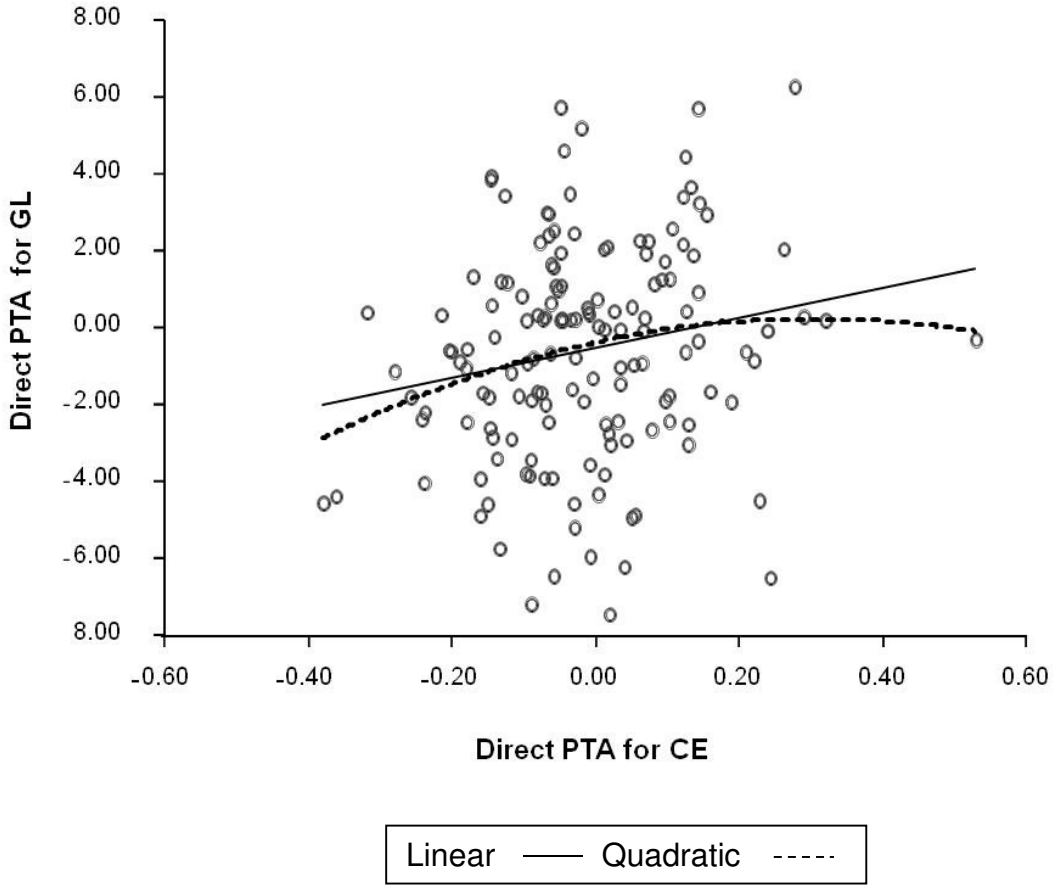


Figure 3.2 Association of direct PTA's obtained from univariate models between gestation length and calving ease

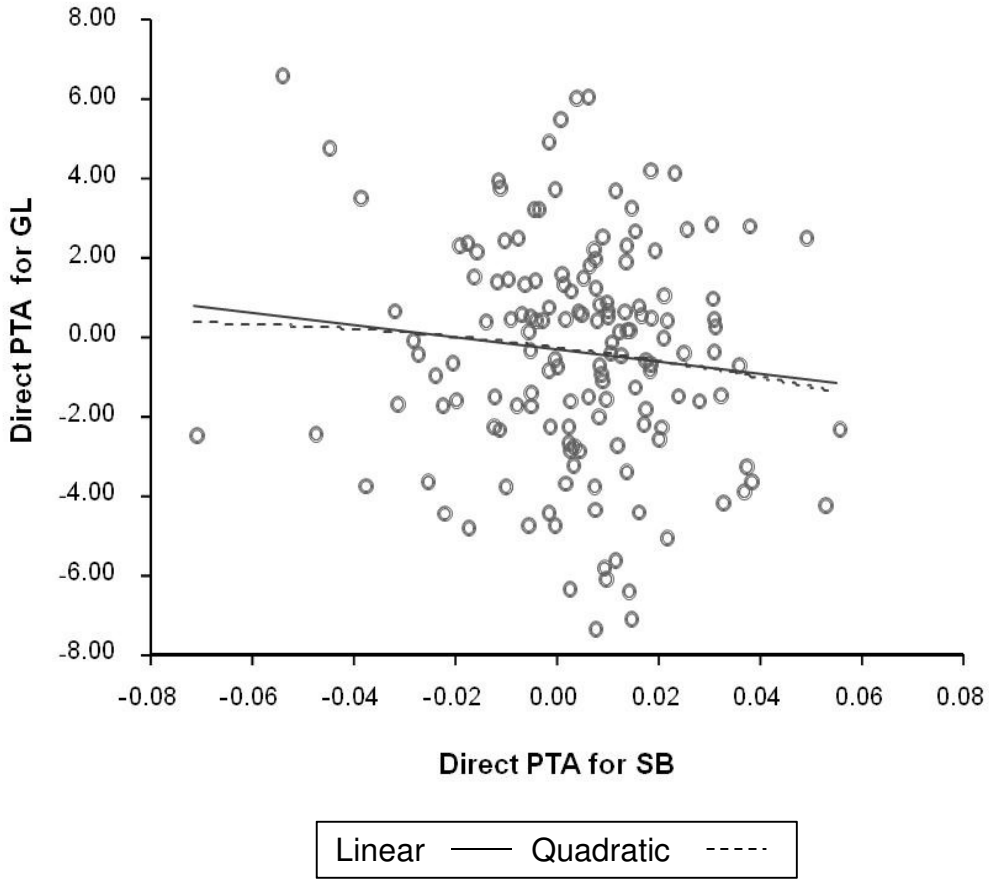


Figure 3.3 Association of direct PTA's obtained from univariate models between gestation length and stillbirth

Table 3.8 Accuracies of prediction1 (r) of average first parity PTA's from 25 young [2] and older[3] sires

	Young sires		Older sires	
	Direct	Maternal	Direct	Maternal
Average progeny group size	88	12	122	101
CE[4]				
Univariate sire-mgs	0.67	0.46	0.68	0.61
Univariate Animal model 1	0.71	0.50	0.72	0.60
Bivariate with GL	0.70	0.52	0.71	0.60
Bivariate with SB	0.71	0.49	0.72	0.64
Bivariate across parities	0.77	0.50	0.82	0.66
GL[4]				
Univariate sire-mgs	0.77	0.69	0.83	0.75
Univariate Animal model 1	0.85	0.45	0.86	0.59
Bivariate with CE	0.86	0.46	0.87	0.59
Bivariate with SB	0.84	0.46	0.86	0.56
Bivariate across parities	0.90	0.78	0.93	0.87
SB[4]				
Univariate sire-mgs	0.31	0.34	0.51	0.54
Univariate Animal model 1	0.39	0.40	0.49	0.48
Bivariate with CE	0.55	0.42	0.65	0.54
Bivariate with GL	0.38	0.46	0.51	0.57
Bivariate across parities	-	-	-	-

[1]For sire-mgs models, values are based on sire and maternal grandsire variances; [2] born between 1999 and 2002; [3] born between 1990 and 1994; [4]CE = calving ease, GL = gestation length, SB = stillbirth

Table 3.9 Prediction error variances of average first parity PTA's from 25 young[2] and older[3] sires

	Young sires		Older sires	
	Direct	Maternal	Direct	Maternal
CE[2]				
Univariate sire-mgs	0.0066	0.0045	0.0066	0.0035
Univariate Animal model 1	0.0261	0.0151	0.0256	0.0135
Bivariate with GL	0.0263	0.0162	0.0266	0.0141
Bivariate with SB	0.0263	0.0132	0.0257	0.0102
Bivariate across parities	0.0689	0.0051	0.0042	0.0038
GL				
Univariate sire-mgs	1.1766	1.1260	0.9087	0.4002
Univariate Animal model 1	3.3837	0.5399	3.2163	1.0350
Bivariate with CE	3.2819	1.2506	3.1916	1.0239
Bivariate with SB	3.6005	1.1877	3.1297	1.0239
Bivariate across parities	0.2367	0.1987	0.1615	0.1287
SB				
Univariate sire-mgs	0.0004	0.0008	0.0003	0.0007
Univariate Animal model 1	0.0014	0.0015	0.0012	0.0012
Bivariate with CE	0.0004	0.0018	0.0365	0.0015
Bivariate with GL	0.0008	0.0025	0.0255	0.0021
Bivariate across parities	-	-	-	-

[1]For sire-mgs models, values are based on sire and maternal grandsire variances; [2] born between 1999 and 2002; [3] born between 1990 and 1994; [4]CE = calving ease, GL = gestation length, SB = stillbirth

3.4. Conclusions

There is additive genetic variance in CE and SB and both traits can thus respond to genetic selection. Heritabilities for CE, SB and GL in UK Holstein cattle were in the range of previously reported genetic parameters for these traits. Both the direct and maternal genetic variances were considerably lower in cows than in heifers. Direct and maternal effects of CE were negatively correlated but this was established only in first parity. CE and SB were genetically highly correlated traits for both direct and maternal components, especially in first parity. GL showed a moderate relationship with CE and SB, which differed between parities but implies that genetically longer gestations are associated with reduced calving performance. The three traits all had high and positive genetic correlations between parities but parities were not demonstrated as being genetically distinct for any trait with the data available. Different between-parity genetic correlations estimated for direct GL and maternal GL emphasize that these are separate traits and thus should be treated as such. Estimates of σ^2_{TBV} indicate that the total additive genetic variance in a calving trait may be lower than the additive direct variance when the genetic direct-maternal covariance is highly negative and the additive maternal variance is small.

Results from this study further demonstrated that estimating genetic parameters for calving traits is complex. Developing a statistical model for a maternally affected trait requires a careful balance between sufficient predictive ability and computational practicality, which in turn are affected by the size of the dataset, potential biases in data recording, the trait in question, computational facilities and the amount of time in hand. However, in general, PTA estimates for calving traits benefitted from multi-trait models. Furthermore, estimates were only slightly less

accurate when a sire-mgs model was fitted instead of an animal model. With the current computing facilities, sire-mgs models exceeded animal models in terms of practicality, as their robustness allowed the analysis of more data and the inclusion of more traits e.g. information from later parities. In the genetic evaluation of calving traits genetic correlations between traits and between parities need to be estimated and the direct-maternal genetic correlation must be considered with caution.

CHAPTER 4:

Evaluating direct and maternal genetic relationships between calving ease, gestation length, and other selection traits in UK Holstein-Friesian heifers.

Adapted from: Eaglen SAE, Coffey MP, Woolliams JA and Wall E 2012. Direct and maternal genetic relationships between calving ease, gestation length, milk production, fertility, type and lifespan of Holstein-Friesian heifers.
Submitted to Journal of Dairy Science

4.1. Introduction

The observed genetic variance estimated for CE in Chapter 3 has shown that although the variance is low, genetic progress can be made and genetic selection can aid in reducing the incidence of difficult calvings in the UK. Consequently, the first CE proofs in the UK were presented as recently as 2010 (Wall et al., 2010), However, if selection on CE will occur, it is important to determine the genetic correlations between CE and other traits of interest. Awareness of functional traits has for a large part increased due to the negative genetic relationships that are observed between production and functional traits (Boichard et al., 2012). These have shown that it is essential for functional traits to be included in national breeding indices to stop undesirable genetic trends on correlated traits. Thus, a genetic evaluation of CE automatically raises the question of how CE is genetically related to other existing (selection) traits of interest as we require knowledge of the underlying genetic relationships to avoid making genetic progress in CE while jeopardising gains in other traits, or vice versa. In this Chapter, we aim to find an answer to that question.

The phenotypic relationships of CE and selection traits such as milk production and fertility are frequently reported and signify the importance of this trait. They were confirmed in more detail in Chapter 2. However, published information on such *genetic* relationships is noticeably lacking. Genetic relationships are generally evaluated through the estimation of genetic correlations. The estimation of genetic correlations, in the case of a maternal trait as CE, however, is complicated by the genetic maternal component. As the phenotype of CE is affected by both a direct and a maternal genetic component, both direct and maternal correlations potentially

exists between CE and other traits and thus the fitted multi-trait statistical model should allow estimation of all separate genetic correlations. Estimation of only a direct or a maternal correlation is likely to result in bias (Willham et al., 1980; Meyer, 1992).A variety of approaches have been taken to avoid this problem (Ali et al., 1983; Dadati et al., 1985; Muir et al., 2004). However, to our knowledge, only two studies have attempted to estimate genetic correlations between CE and other traits by actually separating direct and maternal effects and allowing for the appropriate covariance structure. Firstly, Cue et al. (1990) presented genetic direct and maternal correlations of CE with type traits in a model where sires were assumed to be unrelated, which is likely to have affected the capability of the model to separate all variance components. Secondly, De Maturana (2007) where direct and maternal effects were separated with pedigree included to estimate the genetic relationships between CE, milk yield and fertility.

Besides CE, SB and GL have also been evaluated as being associated with the calving event. In the UK, stillbirth has little detectable genetic variation, whereas GL has been shown to be moderately heritable in both its direct and maternal components which allows for potential genetic selection (Norman et al., 2011; Chapter 3). Possibly, GL affects the dairy cattle industry by affecting calving interval (CI) and milk yield (Hageman et al., 1991; Norman et al., 2011) but reports of genetic correlations between GL and traits of economic importance to dairy production are scarce. Moreover, to our knowledge no study has studied the separate direct and maternal genetic relationships of GL with other traits of interest. In summary, there is a paucity of reliable information on what may be expected when CE or GL is given an emphasis in selection indices, beyond the improvement of the

trait itself. This study therefore has the simple objective of estimating the genetic correlations between CE, GL and established traits of economic interest, namely fertility, milk production, type and lifespan traits, using models that allow the full separation of direct and maternal effects.

4.2. Material and methods

4.2.1. Direct and maternal effects

All models in this thesis follow Willham's (1963) model as described in Chapter 1. Therefore, in this study, when referring to the direct effect of CE (CEd) or GL (GLd), one is addressing the ease of birth or the length of gestation prior to being born respectively. When the maternal effect of CE or GL is mentioned, CEm or GLm, this refers to the ease of calving or the length of gestation prior to calving, respectively.

4.2.2. Data description

The analyses were restricted to first parity CE records. Data composition is described Chapter 1 and data editing is largely described in detail in Chapter 3. The edited calving trait dataset as described in Chapter 3, including the subset of animals recorded both at birth and calving, consisting of 33,051 records, was subsequently matched to the data containing phenotypes of all other traits, which were recorded in the lactation following the recorded calving and extracted from national databases. Selected traits included fertility (CI; days to first service, DFS; non-return rate after 56 days, NR56; number of inseminations per conception, NRINS), milk production (milk yield at day 110 in milk, MY-110; accumulated 305-day milk yield, MY-305; accumulated 305-day fat yield FY-305; accumulated 305-day protein yield, PY-305),

type (udder depth, UD; chest width, CW; rump width, RW; rump angle, RA; mammary composition, MAMC; stature, STAT; body depth, BD) and lifespan traits (functional days of productive life, DPL).

Hence, a merged dataset was created based on a range of cow identification variables e.g. ID, herd, breed, and calving date. Validity checks were performed on the matched dataset to ensure all data was linked to the correct calving event and pedigree information was accurate. Incorrect records were removed and CI was restricted to be between 300-600 days in line with data edits for fertility traits in the UK (Wall et al., 2005). The type traits included were objectively scored by a classifier at inspection. The time between the inspection and the calving dates was restricted to be between 0-8 months. Six out of the seven type traits were objectively scored on a categorical scale of 9, where 1 and 9 are applied to the extremes of the trait as explained by Brotherstone et al. 1990. Scores at the extreme end of the scale represent the following type: CW: 1-narrow, 9-wide; RW: 1-narrow, 9 wide; rump angle RA: 1 – high pin bones, 9 – low pin bones; body depth BD: 1- shallow, 9-deep; stature STAT: 1-small, 9-tall; udder depth UD: 1- below hock, 9-above hock. Mammary composition MAMC is a composite type trait which covers the strength and quality of the fore and rear attachment, strength of central ligament, teat quality and udder texture. MAMC is scored with a pointing system which ranges from <64 – poor to 100 – excellent. All scores were then adjusted for classifier by scaling by the classifier mean and standard deviation to achieve equal means with variances for all classifiers as described by Brotherstone (1994).

The final edited dataset contained 31,053 heifer performance records, originating from 1,757 herds representing 1,951 (service) sires and 2,719 maternal grandsires.

For all records, 5 generations of pedigree records were available. In this dataset, 100% of the records contained phenotypes for CE, and GL, fertility and milk production traits. Type and lifespan data were present in 19% and 46% of the records, respectively. CE frequencies in this dataset are shown in Table 4.1 Missing observations for type and lifespan were recorded as missing. Descriptive statistics of all traits are given by Table 4.2.

Table 4.1 Frequencies and definitions of calving ease (CE) categories

	Score	Frequency	Definition
CE	1	73.13%	1 = easy (non-assisted)
	2	23.05%	2 = moderate – assisted by farmer
	3	3.17%	3 = difficult – assisted by farmer
	4	0.65%	4 = very difficult – assisted by veterinarian

Table 4.2 Descriptive statistics of all traits

Trait	Statistic					
	Min.	Max.	Mean		σ_P^2	
Calving ease (CE)	1	4	1.3	(0.6)	0.4	(0.01)
Gestation length (GL; days)	265	295	281	(5.0)	25	(0.6)
Fertility						
Calving interval (CI; days)	300	600	404	(59)	3286	(35)
Days to first service (DFS; days)	20	200	88	(32)	840	(9)
No. of inseminations to conception (NRINS; #)	1	10	1.9	(1.3)	1.58	(0.02)
Non-return at day 56 after 1st insemination (NR56)	0	1	0.7	(0.5)	0.21	(0.00)
Production						
Actual milk yield at day 110 in milk (MY-110; kg)	5	55	27	(6)	25	(0.3)
Accumulated. actual 305 day milk yield (MY-305; kg)[1]	2754	12349	7523	(1578)	1440	(174)
Accumulated actual 305 day fat yield (FY -305; kg)	71	599	293	(64)	2150	(24)
Accumulated actual 305 day protein yield (PY -305; kg)	65	418	242	(49)	1275	(15)
Type						
Udder depth (UD)	0.4	10.4	5.9	(1.3)	1.4	(0.02)
Mammary composition (MAMC)	67.8	92.0	80.0	(5.0)	21.5	(0.40)
Rump width (RW)	0.4	9.8	5.5	(1.4)	1.6	(0.03)
Rump angle (RA)	0.4	10.5	4.3	(1.3)	1.5	(0.03)
Chest width (CW)	-0.8	9.9	5.2	(1.5)	1.8	(0.03)
Stature (STAT)	0.2	10.9	6.1	(1.4)	1.3	(0.02)
Body depth (BD)	0.4	10.0	5.8	(1.3)	1.4	(0.02)
Lifespan						
Days of productive life (DPL; days)	201	4261	1146	(662)	35	(0.5)

[1] Variance is reported to the power of 10^{-3}

4.2.3. Statistical analyses

Reports on genetic correlations between CE, GL and other traits are scarce. However, reports on genetic correlations between milk production and a variety of other traits, such as fertility and type, are extensive. Therefore, to make results better interpretable and the discussion of results more valuable, MY-305 was fitted as a correlated trait in every analysis. Total days of lactation ranged from 200 to 963 days with a mean of 320 days. Trivariate linear mixed models were fitted using REML, by ASREML version 3.0 (Gilmour et al., 2009), after optional fixed effects and potential interaction effects were tested for significance in SAS v9.1. Chapter 3 demonstrated that the sire-mgs model is the most practical and robust model for the estimation of genetic parameters for calving traits. Therefore, the sire-mgs model was the model of choice for this study.

Phenotypes are recorded on the first parity cow, hence the sire of the cow was fitted to account for the additive direct effect of all but the calving traits. Every calving is affected by both the cow and the calf. This is described by Figure 4.1.

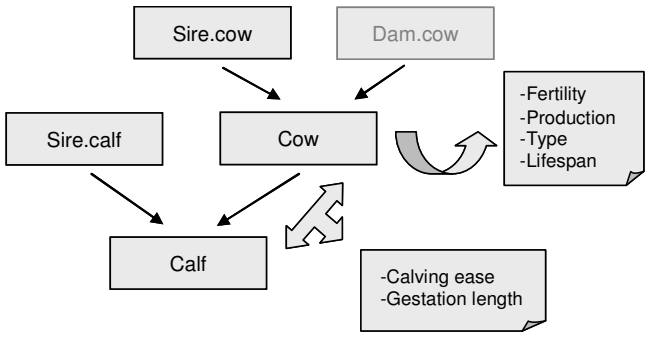


Figure 4.1 Diagram showing the origin of recorded phenotypes

Therefore, for calving traits in the extended sire model it is the sire of the calf that accounts for the additive direct effect, whereas the sire of the cow accounts for the maternal genetic effect. The general linear statistical model fitted therefore equalled

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\\ \mathbf{y}_3\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & 0 & 0\\ 0 & \mathbf{X}_2 & 0\\ 0 & 0 & \mathbf{X}_3\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\\ \mathbf{b}_3\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{1\_sire.calf} & 0 & 0\\ 0 & 0 & 0\\ 0 & 0 & 0\end{bmatrix}\begin{bmatrix}\mathbf{a}_{1\_sire.calf}\\ 0\\ 0\end{bmatrix}+$$
$$\begin{bmatrix}\mathbf{Z}_{1\_sire.cow} & 0 & 0\\ 0 & \mathbf{Z}_{2\_sire.cow} & 0\\ 0 & 0 & \mathbf{Z}_{3\_sire.cow}\end{bmatrix}\begin{bmatrix}\mathbf{a}_{1\_sire.cow}\\ \mathbf{a}_{2\_sire.cow}\\ \mathbf{a}_{3\_sire.cow}\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\\ \mathbf{e}_3\end{bmatrix} \quad , \qquad [4.1]$$

where $\mathbf{y}_i$ is a vector representing the observations for trait 1, trait 2 and trait 3 (trait 1 is consistently either CE or GL, trait 2 is a trait of interest and trait 3 is consistently MY-305). $\mathbf{X}$, $\mathbf{Z}_{i\_sire.calf,}$ and $\mathbf{Z}_{i\_sire.cow}$ are known incidence matrices for non-genetic and sire effects, respectively; $\mathbf{b}$ is a vector of non-genetic effects, $\mathbf{a}_{1\_sire.calf}$ is a vector of the random additive direct effects of the sire of the calf. $\mathbf{a}_{i\_sire.cow}$ is a vector of the random additive effects of the sire of the cow. The random additive effects of the sire of the cow are the direct effects for non-maternal traits and maternal effects for CE and GL, $\mathbf{a}_{1\_sire.calf}$ and $\mathbf{a}_{i\_sire.cow}$ were assumed to follow a multivariate normal distribution, with MVN(0, $\mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A}$) where, $\mathbf{G}_0$ is a 4 x 4 direct-maternal variance-covariance matrix,

$$\mathrm{Var}\begin{bmatrix}a_{1\_sire.calf}\\ a_{1\_sire.cow}\\ a_{2\_sire.cow}\\ a_{3\_sire.cow}\end{bmatrix}=\begin{bmatrix}\sigma^2_{a1\_sire.calf} & & & \\ \sigma_{a1\_sire.calf,sire.cow} & \sigma^2_{a1\_sire.cow} & & \\ \sigma_{a1\_sire.calf,2\_sire.cow} & \sigma_{a1,2\_sire.cow} & \sigma^2_{a2\_sire.cow} & \\ \sigma_{a1\_sire.calf,3\_sire.cow} & \sigma_{a1,3\_sire.cow} & \sigma_{a2,3\_sire.cow} & \sigma^2_{a3\_sire.cow}\end{bmatrix}\otimes\mathbf{A} \qquad [4.2]$$

$\otimes$ is the Kronecker product of matrices, and $\mathbf{A}$ is the relationship matrix; $\mathbf{e}$ is a vector of the residuals, assumed to be MVN(0, $\mathbf{R}\sigma^2_e$), where $\mathbf{R}$ denotes the residual 3 x 3 variance covariance matrix and σ^2_e is the residual variance. So, for every bull,

four breeding values are estimated: a direct breeding value for CE or GL ($a_{1\_sire.calf}$), a maternal breeding value for CE or GL ($a_{1\_sire.cow}$), a direct breeding value for trait *i* ($a_{2\_sire.cow}$) and a direct breeding value for MY-305 ($a_{3\_sire.cow}$). Generally, for calving, fertility and production traits the non-genetic effects fitted in the model included sex of the calf, herd, the main effects and interaction effect of year and month of calving, a linear covariate of age of the dam (months), and a random effect of herd-year. A potential quadratic effect of age of dam on CE and GL was checked but not detected. Additional fixed effects fitted for the type traits included: the main effects and interaction effect of year and month of inspection, the stage of lactation at inspection, the age at inspection (months) as a covariate and a quadratic effect of age at inspection. For lifespan traits an additional quadratic effect of age at calving (months) was included in the model.

As equation 2 and 3 indicate, the co(variances) estimated by an extended sire model are sire variances. These are then algebraically converted into direct and maternal variance components. The mathematical equations for this conversion are given in Appendix A, page 170. Significance of the estimated co(variances) was generally tested by a confidence interval of 1.96*s.e. (P-value 0.05). However, critical values e.g. estimates with P-values close to 0.05 (0.05-0.06) were tested on significance by a likelihood ratio test with the critical value of 2.79 (Stram et al., 1994). The trivariate analyses between calving traits, MY-305 and NR56 did not converge. MY-305 was therefore replaced by MY-110 in this specific analysis to allow convergence. Studies on GL have reported potential non-linear relationships of GL and other traits (Hansen et al., 2004; Norman et al., 2010). In case of a non-linear relationship, correlation estimates obtained by a linear multi-trait model may be

obscured. In this study, relationships between traits were tested for non-linearity by plotting PTA's obtained from univariate models against each other. In addition, potential obscured genetic correlations with GL were double checked by reanalyses of all trivariate models fitting GL on a folded scale. This scale was created by rescaling the GL scale as such: 295 = 265, 294 = 267, 293 = 266 etc., as in Wall et al. (2005).

4.3. Results

4.3.1. Genetic correlations with calving ease

4.3.1.1. Fertility traits

Estimated genetic correlations between CE and fertility traits, presented in Table 4.3, show that the ease of calving, CEm, is favourably associated with NRINS (0.83±0.20) and CI (0.67±0.22), but not with DFS. This implies that, genetically, a difficult calving is not associated with a delay in time to breeding but rather with the inability to conceive. The ease of birth, CEd, is found to be correlated to NR56 (0.67±0.27), suggesting that a more difficult birth is genetically associated with a lower probability of returning to oestrus within 56 days after first insemination, in first lactation (Figure 3.1). Estimated heritabilities for fertility traits are low ranging from ±0.014 for NR56 (n.s.) to ±0.070 for DFS, which is in line with literature estimates (Wall et al., 2005)

4.3.1.2. Production traits

A moderate positive genetic correlation was detected between CEm and milk production in first lactation (0.34±0.15; Table 4.3) suggesting that individuals with high genetic merit for milk production are genetically prone to a more difficult first

calving. CEm also shows to be significantly correlated to FY-305 (0.39±0.13). The positive relationship with FY-305 implies that individuals genetically prone to more difficult first calvings are also genetically prone to a higher fat yield produced in the subsequent lactation. The ease of birth (CEd) was also genetically correlated with milk production. A significant negative genetic correlation was estimated between CEd and MY-110 (-0.45±0.13) and between CEd and MY-305 (-0.44±0.12), suggesting that, genetically, individuals with the genetic merit for a relatively low milk yield in first lactation are genetically predisposed to be born with more difficulty, supporting associations found in Chapter 2. Similarly, CEd was genetically negatively associated with FY-305 (-0.60±0.13) and accumulated actual 305-day protein yield (PY-305; -0.46±0.13). Hence, more difficult births are genetically associated with a lower fat and protein yield in first lactation as adult heifers (Figure 3.1). Estimated heritabilities for milk production traits were estimated as 0.33 for MY-110, ±0.49 for MY-305, 0.35 for FY-305 and 0.43 for PY-305 and conform to literature (Berry et al., 2004).

4.3.1.3. Type traits

Results in Table 4.4 demonstrates that the ease of calving, CEm, is genetically related to two out of seven type traits. A significant genetic correlation was found with CW (0.55±0.20) and BD (0.47±0.18). The positive sign indicates that more difficult calvings are genetically associated with wider chests and deeper bodies. No significant genetic correlations were detected between CEd and type suggesting that difficult births, out of heifer dams, are not related to the type traits recorded in first lactation. The heritabilities of type traits shown by Table 4.4 and 4.6 demonstrate that type traits are moderately heritable. Estimated heritabilities range from 0.24 for

UD to 0.41 for STAT and are all in line with the literature on type traits (Brotherstone et al., 1990; Cue et al., 1990)

4.3.1.4. Lifespan traits

No significant genetic correlations were detected for CE with DPL, suggesting that, from the results obtained in this study, it cannot be concluded that either the ease of birth or the ease of calving is genetically related to the length of productive life (Table 4.4). The heritability of DPL was estimated at 0.11±0.02, which is at the higher end of the range reported for lifespan in the literature: 0.025 to 0.166 (Forabosco et al., 2008).

Table 4.3 Genetic parameters following the trivariate analyses of calving ease, accumulated 305-day milk yield, fertility and production traits

Trait	h^2	σ_A^2	Genetic correlation with CE		Genetic correlation with MY-305[2]
			r_{CEd}	r_{CEm}	r
Calving					
CE – direct	0.10 (0.02)*	0.02 (0.01)	1.00 (0.00)	-0.38 (0.18)*	-0.42 (0.16)*
CE – maternal	0.04 (0.02)*	0.01 (0.00)	-0.38 (0.18)*	1.00 (0.00)	0.27 (0.18)
Fertility					
CI	0.03 (0.01)*	111 (39)	-0.51 (0.24)*	0.67 (0.22)*	0.61 (0.13)*
DFS	0.06 (0.02)*	50 (13)	-0.34 (0.21)	0.21 (0.23)	0.46 (0.11)*
NRINS	0.02 (0.01)*	0.04 (0.01)	-0.24 (0.26)	0.83 (0.20)*	0.41 (0.16)*
NR56[2]	0.01 (0.01)	0.003 (0.01)	0.67 (0.27)*	-0.54 (0.31)	-0.13 (0.21)[2]
Production					
MY-110	0.33 (0.03)*	7.9 (0.8)	-0.45 (0.13)*	0.27 (0.16)	0.99 (0.00)*
MY-305[1]	0.49 (0.04)*	0.7 (0.1)	-0.44 (0.12)*	0.34 (0.15)*	1.00 (0.00)*
FY -305	0.35 (0.03)*	764 (78)	-0.60 (0.11)*	0.39 (0.13)*	0.74 (0.03)*
PY -305	0.43 (0.04)*	550 (51)	-0.46 (0.13)*	0.38 (0.17)	0.92 (0.01)*

* $P < 0.05$

[1] Variances are reported to the power of 10^{-4}

[2] The analysis of NR56 is conducted with the correlated trait of accumulated 110-day milk yield, MY -110, to allow convergence.

Table 4.4 Genetic parameters following the trivariate analyses of calving ease, accumulated 305-day milk yield, type and lifespan traits

Trait	h^2	σ_A^2	Genetic correlation with CE		Genetic correlation with MY-305
			r_{CEd}	r_{CEm}	r
Type					
UD	0.24 (0.05)*	0.33 (0.07)	-0.13 (0.18)	-0.20 (0.20)	-0.47 (0.09)*
MAMC	0.26 (0.05)*	5.8 (1.13)	-0.21 (0.17)	0.15 (0.19)	0.40 (0.09)*
RW	0.33 (0.05)*	0.54 (0.10)	-0.07 (0.17)	0.29 (0.18)	0.17 (0.10)*
RA	0.39 (0.06)*	0.60 (0.10)	0.01 (0.20)	0.22 (0.17)	0.09 (0.09)
CW	0.20 (0.04)*	0.37 (0.09)	-0.10 (0.18)	0.55 (0.20)*	-0.02 (0.11)
STAT	0.41 (0.06)*	0.56 (0.09)	0.03 (0.15)	-0.02 (0.17)	0.24 (0.09)*
BD	0.32 (0.05)*	0.44 (0.07)	-0.06 (0.16)	0.47 (0.18)*	0.22 (0.09)*
Lifespan					
DPL[1]	0.11 (0.02)*	3.74 (0.84)	-0.34 (0.20)	0.38 (0.21)	-0.46 (0.10)*

* $P < 0.05$

[1] Variances are reported to the power of 10^{-4}

4.3.2. Genetic correlations with gestation length

For all traits, potential non-linearity with GL was tested by repetition of each model with a 'folded' phenotypic value of GL (Wall et al., 2005). No proof of non-linearity was found in the relationships between GL and all other traits. Use of the linear multi-trait model was therefore classed as appropriate.

4.3.2.1. Fertility traits

The majority of correlations between GL and fertility traits (Table 4.5) were not significant, implying that the length of gestation (either prior to being born or prior to giving birth) does not genetically relate to subsequent fertility in first lactation. The significant genetic correlation between GLm and NRINS (-0.47±0.23) however suggests that relatively long gestations periods prior to giving birth genetically correlate to less services to conception.

4.3.2.2. Production traits

Table 4.5 shows that the length of gestation prior to giving birth, GLm, is not genetically related to milk production in first lactation, whereas the length of gestation prior to being born, GLd, is. Significant negative correlations between GLd and MY-110 (-0.22±0.10) and GLd and MY-305 (-0.19±0.09) suggest that calves that are *in utero* for a relatively long period before they are born have lower milk yields in their first lactation as adult heifers. This is consistent with the equivalent correlation of CEd and milk production. GLd was also found to correlate genetically to PY-305 (-0.22±0.10) but not to FY-305.

4.3.2.3. Type traits

GLm shows a genetic correlation with type. Table 4.6 presents the significant correlations of GLm with RW (0.52±0.15) and STAT (0.48±0.15) suggesting that longer gestation periods prior to giving birth, are genetically related with wider rumps and increased stature. There were no significant genetic correlations found between GLd and type. Hence, from results obtained in this study, it cannot be concluded that time of gestation prior to being born is genetically related to the type traits scored in first lactation.

4.3.2.4. Lifespan traits

No significant genetic correlations were detected between GL and DPL, suggesting that from the results obtained in this study, it cannot be concluded that either the gestation length prior to birth or calving is genetically related to the length of productive life (Table 4.6).

Table 4.5 Genetic parameters following the trivariate analyses of gestation length, accumulated 305-day milk yield, fertility and production traits

Trait	h^2	$\sigma^2_{A_D}$	Genetic correlation with GL		Genetic correlation with MY-305[2]
			r_{GLd}	r_{GLm}	r
Calving					
GL - direct	0.49 (0.05)*	12.1 (1.5)	-0.30 (0.13)*	1.00 (0.00)	-0.19 (0.09)*
GL - maternal	0.09 (0.03)*	2.1 (0.6)	1.00 (0.00)	-0.30 (0.13)*	0.04 (0.14)
Fertility					
CI	0.02 (0.01)*	98 (31)	0.19 (0.20)	-0.29 (0.26)	0.61 (0.14)*
DFS	0.07 (0.02)*	58 (14)	-0.06 (0.15)	-0.16 (0.21)	0.42 (0.10)*
NRINS	0.02 (0.01)*	0.03 (0.01)	0.33 (0.20)	-0.47 (0.23)*	0.29 (0.17)
NR56[2]	0.01 (0.01)	0.001 (0.00)	0.18 (0.37)	0.30 (0.54)	-0.22 (0.34)[2]
Production					
MY-110	0.32 (0.03)*	6.8 (0.7)	-0.22 (0.10)*	0.03 (0.15)	0.99 (0.00)*
MY-305[1]	0.50 (0.04)*	0.7 (0.1)	-0.19 (0.09)*	0.04 (0.14)	1.00 (0.00)*
FY-305	0.36 (0.03)*	788 (74)	-0.13 (0.10)	-0.10 (0.15)	0.72 (0.03)*
PY-305	0.46 (0.04)*	595 (50)	-0.22 (0.10)*	-0.01 (0.15)	0.92 (0.01)*

* $P < 0.05$

[1] Variances are reported to the power of 10^{-4}

[2] The analysis of NR56 is conducted with the correlated trait of accumulated 110-day milk yield, not 305; MY -110, to allow convergence.

Table 4.6 Genetic parameters following the trivariate analyses of gestation length, accumulated 305-day milk yield, type and lifespan traits

Trait	h^2	$\sigma^2_{A_D}$	Genetic correlation with GL		Genetic correlation with MY-305
			r_{GLd}	r_{GLm}	r
Type					
UD	0.18 (0.04)*	0.25 (0.05)	-0.07 (0.14)	0.31 (0.18)	-0.45 (0.09)*
MAMC	0.23 (0.04)*	4.92 (0.95)	-0.14 (0.13)	0.19 (0.18)	0.41 (0.09)*
RW	0.28 (0.05)*	0.45 (0.08)	0.09 (0.13)	0.52 (0.15)*	0.21 (0.09)*
RA	0.40 (0.06)*	0.60 (0.09)	0.09 (0.12)	-0.18 (0.16)	0.10 (0.09)
CW	0.20 (0.04)*	0.35 (0.07)	-0.09 (0.14)	0.35 (0.18)	-0.03 (0.11)
STAT	0.41 (0.05)*	0.53 (0.08)	-0.11 (0.12)	0.48 (0.14)*	0.20 (0.08)*
BD	0.32 (0.05)*	0.44 (0.07)	-0.10 (0.12)	0.28 (0.16)	0.25 (0.09)*
Lifespan					
DPL[1]	0.11 (0.02)*	3.70 (0.86)	0.09 (0.15)	-0.23 (0.20)	-0.45 (0.11)*

* $P < 0.05$

[1] Variances are reported to the power of 10^{-4}

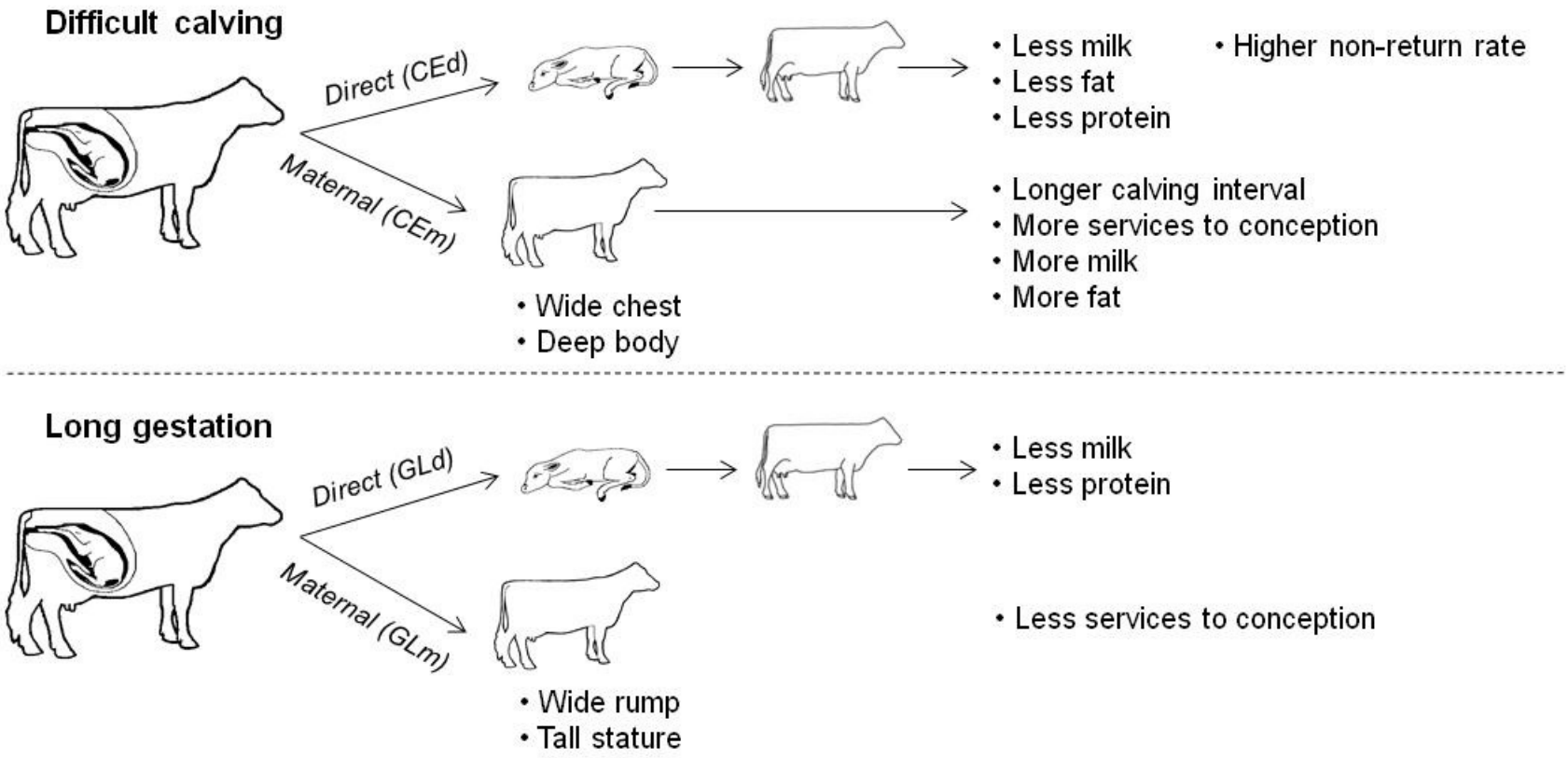


Figure 4.2 Diagrammatic representation of the genetic relationships between a difficult calving or long gestation with milk production, fertility and type

4.4. Discussion

The study has (i) provided new understanding on the genetic relationship of calving events with milk production, fertility, and type traits; (ii) allowed us to better characterise individuals and their potential problems, as presented in Figure 4.2; and (iii) provided validation of previously established genetic relationships among milk production, fertility and type traits. In what follows, we choose not to elaborate on the genetic correlations across the calving traits themselves as this has been discussed extensively by Chapter 3 and estimates agree well between studies. Please do note that in this study, the pooled genetic correlation between GLd and GLm is estimated to be negative and significant. Note in the interpretation of the estimated correlations that CE was scored on a scale which increases with difficulty (Chapter 1). Hence, a higher CE score represents a more difficult calving.

4.4.1. Genetic correlations with calving ease

A difficult calving, as a maternal trait, is associated with a high milk yield, wide and deep conformation score and relatively poor fertility (Figure 4.2). The type and fertility descriptions match literature descriptions of a high producing cow (Berry et al., 2004) which gives confidence in the conducted analysis. The relatively high standard error on the estimated correlation between CEm and 305-MY may support the recent evidence of the relatively weak phenotypic association between a cows' ease of calving and her subsequent milk production given in Chapter 2 (Berry et al., 2007). Considering the phenotypic association found in Chapter 2 between CEm and the first 90 days of lactation, one might have expected a genetic correlation between CEm and MY-110. This genetic correlation was however not detected suggesting

that the association found in Chapter 2 (CEm-first 90 days of lactation) is primarily environmental. The moderate positive genetic correlation between CEm and 305-MY contradicts the low negative estimate reported by De Maturana et al. (2007) although the data of De Maturana et al. contains a total of 8 lactations whereas this study focussed on first lactation CE only. Considering the difference in prevalence and genetic variances between first and later CE (Chapter 1 and 3) it is plausible that the genetic relationship of CE with milk production differs between lactations.

In the literature, narrow rumps and a low rump angle (e.g. high pin bones) are generally considered unfavourable for calving ease (Philipsson et al., 1976; Wall et al., 2005). This study did not detect significant genetic correlations between RW, RA and CE. Results therefore suggest that the reported phenotypic associations are primarily environmental and therefore contradict findings by Dadati et al. (1985) and Thompson et al. (1980). The results are, however, supported by Naazie et al. (1990) who reported a very weak genetic relationship between pelvic dimensions and calving difficulty. The lack of consensus on these specific genetic correlations is also shown by Ali et al. who contradicts general consensus by reporting a positive genetic correlation between hip width and CE (wider hips, more calving difficulty). The differences in statistical models used in these different studies may have contributed to the various outcomes of estimation. For example, direct and maternal effects might not have been 'decomposed' or sires were assumed to be unrelated (Ali et al., 1983; Dadati et al., 1985; Cue et al., 1990).

This study has shown that individuals who are born with difficulty are associated with poor genetic merit for milk production (Figure 4.2, CE as a direct trait). It thereby provides a genetic underpinning to the evidence of a phenotypic relationship

between the ease of birth of a female calf and her subsequent milk production as an adult cow as established in Chapter 2 and by Heinrichs et al. (2011). Contrary to our results however, Maturana et al. (2007) reports a weak negative genetic correlation between CEd and milk production, although their s.e. is of such magnitude that a positive correlation cannot be ruled out. A conjecture arising from the results on relationships with fertility is that the unfavourable negative correlations established between CEd and fertility are mediated through the positive correlation of CEd with milk production. Hence, good direct calving ease is genetically associated with high milk yield which in turn is negatively correlated to fertility.

The positive genetic correlation between CEd and NR56 found here demonstrates how misinterpretation can occur if there is no decomposition of the direct and maternal genetic effects. For example, Muir et al. (2004) estimate a genetic correlation between CE (direct and maternal combined) and NR56 to be positive. This is then interpreted as reflecting the correlation of NR56 with CE as a maternal trait, which in this study is shown to be negative (Table 4.3). The positive correlation found by Muir et al. can be explained by their model as the total genetic correlation of CE with NR56 is

$$r_g = \frac{(\sigma_{A_{CEd,NR56}} + \sigma_{A_{CEm,NR56}})}{\sqrt{\sigma^2_{TBV_{CE}}}^{*}\sqrt{\sigma^2_{A_{NR56}}}} \qquad [4.3]$$

where σ^2_{TBV} is as Equation [1.6] (Chapter 1). This results in a positive estimate (0.37 ± 0.25). Hence, the genetic correlation reported by Muir et al. consists in part of the correlation between CEd and NR56, (which in this study is negative) as the fitted model in Muir et al. does not allow for the separation of direct and maternal effects.

4.4.2. Genetic correlations with gestation length

Although the genetic variances of GL are considerable, the results of this study suggest that the trait is perhaps best used for multi-trait models to improve predictive ability, such as in Chapter 3, rather than direct selection for the trait itself. The genetic relationships established for GLd and GLm seem to be limited to milk production and type (Figure 4.2) whereas phenotypic associations are found more often (e.g. CI, days open, milk yield, DPL; Norman et al., 2009, 2010).

The direct genetic correlations with GL indicate that early born individuals are likely to have good merit for milk production whereas the maternal correlations suggest that long-carrying animals are large with wide rumps. The lack of a significant genetic correlation between GLm and milk production contrasts with previous phenotypic evidence of long gestation periods being related to high milk yield (Norman et al., 2011). There is a greater consensus over the negative relationship of GLd with milk production. Norman et al. (2009) reports a decrease in length of productive life as PTAs for GLd increase although their methodology varies greatly from this study. The greater knowledge of phenotypic and genetic relationships from this study widens the discussion on how selection on GL could benefit the dairy cattle industry. The economic importance of GL lies mainly in its association with CI, and its potential relationship with milk production (Norman et al., 2011). The relationship with CI described in this study however is shown to be principally environmental while the genetic relationship with milk production traits is shown to be complex. Furthermore, the phenotypic relationships reported for a range of functional traits (e.g., calving ease, stillbirth, fertility) show an optimum performance at intermediate GL (e.g. a very short or long gestation is unfavourable, Norman et al.,

2010). Therefore, selecting on direct GL to achieve benefits in milk production appears irrational as any gains in either lengthening or shortening of GL are likely to be counteracted by detrimental effects in other important functional traits.

4.5. General discussion

This study serves to fill a fundamental gap in knowledge about the genetic interrelationships of CE and GL in UK Holstein-Friesian heifers with several important (selection) traits in dairy cattle breeding. It allows the impact of future breeding objectives to be reliably predicted and demonstrates the value of estimating both direct and maternal relationships for these predictions. The estimation of maternal genetic parameters is however complex and the results of any statistical model incorporating a maternal effect therefore require careful consideration (Chapter 1). In this study, Tables 4.3 to 4.6 show large standard errors on the majority of estimated co(variances) which is probably a direct result of the model attempting to separate a large number of variance components using a limited amount of information given by the dataset and pedigree. Furthermore, the results show a general tendency for the direct and maternal relationships to be opposite in sign. Similar trends were shown by Cue and Hayes (1990). As it is a consistent trend across a variety of traits, it cannot be ruled out that this phenomenon is an artefact of the fitted model. However, the fact that the vast majority of genetic parameters yielded by the model are in line with estimates in literature which are obtained by a variety of statistical models speaks strongly for its robust validity. It has also been demonstrated that not all previously observed associations of selection traits with CE and GL have a direct genetic base. For example, no significant genetic correlation was detected between DPL with CE and GL despite the many reports of complications during first calving considerably increasing the culling risk of individuals (Beaudeau et al., 2000; De Maturana et al., 2007). Furthermore, despite a report of a phenotypic association between GL and milk production (Norman et al.,

2011), there was no evidence of a genetic correlation between GLm and subsequent milk production. It is however possible that the genetic correlation of GL as a *direct* trait with milk production has contributed to the association that was found by Norman et al. (2011). An important aspect of this study is therefore the partitioning of genetic relationships into the direct and maternal genetic covariance components to allow for a more detailed evaluation of what is, or is not, underlying the phenotypic observations. This is not only crucial for the inclusion of calving traits in national breeding goals but is also essential for our understanding of how calving performance has been influenced by selection in the past and how it will respond to selection in the future.

4.6. Conclusions

CE and GL in first parity UK Holstein-Friesian dairy cattle are genetically related to other important (selection) traits in dairy cattle breeding. This needs to be considered if selection for CE and GL are to be implemented into national breeding goals. As yet, however, results suggest that GL may be of better value to the dairy cattle industry as an indicator trait, rather than novel selection trait of economic value.

The separation of direct and maternal genetic effects in the estimation of genetic correlations between calving traits and other traits leads to a more precise evaluation of genetic interrelationships underlying observed phenotypic associations. This is essential for understanding the role of genetic selection in the current state of calving performance in first parity UK dairy cattle, and appropriately applying genetic selection upon calving traits in the future.

Easily born individuals are genetically prone to high milk yield and reduced fertility in first lactation. Difficult calving heifers are likely associated with being high producing, wide and deep animals with a reduced ability to subsequently conceive. Individuals that are born relatively early are associated with good genetic merit for milk production. And finally, individuals carrying their young longer are genetically associated with being wide and large animals that were born relatively early themselves.

CHAPTER 5:

Improving the genomic model for calving ease in the UK

Eaglen SAE, Mrode R, Coffey MP, Woolliams JA and Wall E 2012.

5.1 Introduction

Genomic selection (Meuwissen et al., 2001) offers great potential for the genetic improvement of dairy cattle by promising to overcome two of its main limitations for genetic progress i.e. accuracy and generation interval. As statistical algorithms and computing power now allow rapid processing of genomic data, and large reference populations have been built, an increasing number of countries have started to predict and publish genomic breeding values for dairy bulls. It is suggested that the potential advantages of genomic selection will be highest for traits where making genetic progress through traditional selection is most difficult such as fertility traits and maternal traits (Goddard et al., 2007). Indeed, the potential of genomic selection to increase accuracy without increasing generation interval bears great promise for a maternal trait such as CE. It is therefore logical that in this thesis, where the potential of genetic selection on CE is explored, we also give attention to *genomic* selection on CE. In the UK, the first genomic breeding values were officially published in April 2012 (personal communication, R.Mrode), including genomic breeding values on CE.

Yet, as any gain of genomic selection will depend on the accuracy of predicted genomic breeding values we aim to answer the following question in this Chapter: 'Can the current UK genomic model for CE be improved to increase the accuracy of estimated direct genomic values?'

The prediction of genomic breeding values conceptually involves two phases. Firstly, the estimation of single nucleotide marker (SNP) effects on the phenotypes of a genotyped reference population and secondly, the prediction of genetic merit of selection candidates with the knowledge of their genotypes and estimated marker

effects (Hayes, 2009). Algorithms for genomic prediction are still developing, however genomic predictions performed for national genetic evaluations typically use BLUP and mixed model methods. These build upon conventional mixed model equations adapted to analyze genomic data (Meuwissen, 2001), either in two steps (ridge regression) or one (genomic BLUP; gBLUP). In application to dairy cattle, data typically consists of de-regressed proofs (DRPs) which serve as surrogate 'phenotypes', and are assumed to be free of systematic effects other then genetic value (Garrick et al., 2009).

Just like conventional maternal models, such as the ones fitted in Chapter 3 and 4, genomic models also need to take into account both the direct and the maternal component of CE. However, given the early stage of development in genomic prediction models little attention has been given to the fitting of indirect genetic effects such as the maternal effect in CE. Production traits without indirect effects are statistically simpler and the same models are likely to fit complex traits such as CE sub-optimally which could result in poor estimation of direct genomic values (DGVs) for CE. The objective of the study described in this Chapter is to evaluate the added value of adjusting the current genomic model for CE in the UK such that it suits the genetic characteristics of a maternal trait better by incorporating a direct-maternal genetic relationship. To do so, single trait (ST) gBLUP models were compared to multi-trait (MT) gBLUP models whilst fitting direct and maternal de-regressed proofs as correlated traits Furthermore, the consequences of a ST de-regression of CEd and CEm proofs were evaluated by conducting a MT de-regression which again allows for a direct-maternal relationship. Analyses were subsequently repeated fitting the calculated multiple-trait DRPs. Accuracies of

DGVs obtained from all models were assessed by the correlations between estimated DGVs and DRPs for a separate validation population

5.2. Material and methods

5.2.1. Data

As a result of cooperation through DairyCo with the Cooperative Dairy DNA Repository (CDDR), ANAFI (Italy), the UK industry and SAC, data from 11480 bulls, genotyped with the Illumina bovine 50k SNP chip, were available for analyses. Data were edited to allow a minor allele frequency of 0.05, the call rate for animals was 95% (across the various chips) and checks for Mendelian inconsistency were carried out. A remaining total of 41,703 SNPs were selected for genomic evaluations. Sire proofs for direct CE (CEd) and maternal CE (CEm) from the UK official April 2012 run (UK bulls) and MACE phenotypic proofs (USA bulls) were de-regressed and used as dependent variable in the genomic analyses. The software MiX99 (Lidauer et al., 2011) was used for the de-regression using a full animal pedigree. Effective daughter contributions (EDCs) were used as weights to account for varying reliabilities among individuals. Generally, in the UK, CEd and CEm are de-regressed separately, following a univariate de-regression model as described by Jairath et al. (1997). Hence, the traits are assumed to be independent at de-regression. Bulls born before 2006 were used as a reference population, and thus to estimate the SNP effects for direct and maternal calving ease. Bulls born after 2006 were used as the validation population, hence DRPs were set to missing to simulate the evaluation of juvenile sires. All bulls were required to have at least 10 EDCs and a reliability of at least 59%. Reference populations consisted of 4,556 bulls for CEd and 4,553 for

CEm respectively. Validation populations contained 1,333 and 532 bulls for CEd and CEm, respectively. Average EDC equalled 105 for CEd (range: 13-10,441) and 99 for CEm (range: 11-3,861).

5.2.2. Methods

5.2.2.1. Single trait gBLUP model (STgBLUP)

For the univariate estimation of DGVs the following univariate gBLUP model was fitted

$$\mathbf{y}_i = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e} \qquad [5.1]$$

where $\mathbf{y}_i$ is a vector of DRPs for either CEd or CE. As fixed effects were already accounted for **Xb** reduced to $\mathbf{1}_n\mu$ where $\mathbf{1}_n$ is a vector of ones and μ is the mean, **Z** is a known incidence matrix linking DRPs to bulls, **g** is a vector of additive CEd or CEm genomic effects for bulls in the reference and validation population and **e** is a vector of residuals, with $\mathbf{e} \sim N(0, \mathbf{I}\,\sigma^2_e)$, where σ^2_e equals the residual variance.

The mixed model equations are

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z}+\mathbf{G}^{-1}\alpha \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{g}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \end{bmatrix} \qquad [5.2]$$

where $\mathbf{G}^{-1}$ is an inverse genomic relationship matrix, replacing the conventional pedigree relationship matrix (**A**) and $\hat{\mathbf{g}}$ is a vector of estimated DGVs for either CEd or CEm. Scalar α equals σ^2_e / σ^2_g in which σ^2_g represent the genetic variance for this model. **G** was constructed by the first method described in VanRaden (2008)

$$\mathbf{G} = \frac{\mathbf{ZZ'}}{2\Sigma p_i(1-p_i)} \qquad [5.3]$$

where **Z** follows from a subtraction of 2 matrices, **M** and **P**. **M** represents an incidence matrix that specifies which alleles each individual inherited and matrix **P**

contains the allele frequencies expressed as a difference from 0.5 and multiplied by 2. Subtraction of **P** from **M** sets the expected value of μ to zero and gives more credit to rare alleles than to common alleles when calculating genomic relationships (Clark et al., 2011), p_i is the frequency of the second allele at locus *i* and division by $2\Sigma p_i(1-p_i)$ scales **G** to be analogous to **A** (VanRaden, 2008). Vector **g** is assumed to follow a normal distribution, $\mathbf{g} \sim N(0, \mathbf{G}\sigma^2_g)$ in which σ^2_g represent the additive genetic variance for either CEd or CEm. σ^2_g and σ^2_e were fixed to sire genetic variances and residual variances used for national genetic evaluations of CEd and CEm respectively which are listed in Table 5.1 along with the heritabilities.

Table 5.1 Genetic parameters used for the de-regression of sire proofs and for the prediction of DGVs

Parameter	
σ^2_{sire}	0.0104
σ^2_{mgs}	0.0046
$\sigma_{sire,mgs}$	0.0005
h^2_{direct}	6.8%
$h^2_{maternal}$	4.4%
$\boldsymbol{r}_{\boldsymbol{g}_{direct,maternal}}$	-0.57
σ^2_e	0.4291

5.2.2.2. Multi-trait gBLUP model (MTgBLUP)

The following bivariate gBLUP model was fitted

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & 0\\ 0 & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1 & 0\\ 0 & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{g}_1\\ \mathbf{g}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} \quad [5.4]$$

where y1 and y2 represent DRPs for CEd and CEm respectively and where the vectors and incidence matrices correspond to those in the univariate gBLUP model. Least square equations are

$$\begin{bmatrix} \mathbf{X}_1'r^{11}\mathbf{X}_1 & \mathbf{X}_1'r^{12}\mathbf{X}_2 & \mathbf{X}_1'r^{11}\mathbf{Z}_1 & \mathbf{X}_1'r^{12}\mathbf{Z}_2 \\ \mathbf{X}_2'r^{21}\mathbf{X}_1 & \mathbf{X}_2'r^{22}\mathbf{X}_2 & \mathbf{X}_2'r^{21}\mathbf{Z}_1 & \mathbf{X}_2'r^{22}\mathbf{Z}_2 \\ \mathbf{Z}_1'r^{11}\mathbf{X}_1 & \mathbf{Z}_1'r^{12}\mathbf{X}_2 & \mathbf{Z}_1'r^{11}\mathbf{Z}_1+\mathbf{G}^{-1}k^{11} & \mathbf{Z}_2'r^{12}\mathbf{Z}_1+\mathbf{G}^{-1}k^{12} \\ \mathbf{Z}_2'r^{21}\mathbf{X}_1 & \mathbf{Z}_2'r^{22}\mathbf{X}_2 & \mathbf{Z}_2'r^{21}\mathbf{Z}_1+\mathbf{G}^{-1}k^{21} & \mathbf{Z}_2'r^{22}\mathbf{Z}_2+\mathbf{G}^{-1}k^{22} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}}_1 \\ \hat{\mathbf{b}}_2 \\ \hat{\mathbf{g}}_1 \\ \hat{\mathbf{g}}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1'r^{11}\mathbf{y}_1+\mathbf{X}_2'r^{12}\mathbf{y}_2 \\ \mathbf{X}_2'r^{21}\mathbf{y}_1+\mathbf{X}_2'r^{22}\mathbf{y}_2 \\ \mathbf{Z}_1'r^{11}\mathbf{y}_1+\mathbf{Z}_1'r^{12}\mathbf{y}_2 \\ \mathbf{Z}_2'r^{12}\mathbf{y}_1+\mathbf{Z}_2'r^{11}\mathbf{y}_2 \end{bmatrix} \quad [5.5]$$

where k^{ij} are elements of $\mathbf{K}^{-1}$, $\mathbf{K} = \begin{bmatrix} k11 & k12 \\ k21 & k22 \end{bmatrix} = \begin{bmatrix} \sigma^2_{g_d} & \sigma_{g_{dm}} \\ \sigma_{g_{dm}} & \sigma^2_{g_m} \end{bmatrix}$ and r^{ij} are elements of $\mathbf{R}^{-1} = \begin{bmatrix} r^{11} & r^{12} \\ r^{21} & r^{22} \end{bmatrix} = \begin{bmatrix} \sigma^2_{e1} & \sigma_{e12} \\ \sigma_{e21} & \sigma^2_{e2} \end{bmatrix}^{-1}$.

Similarly to the univariate gBLUP model, all genetic variance components were fixed to conventional additive direct and maternal (co)variance components used in UK genetic evaluations for CE (Table 1).

5.2.2.2.1. Residual covariance matrix

As CEd and CEm are fitted as correlated traits, the MTgBLUP model expects a residual variance covariance matrix containing a residual direct variance, a residual maternal variance and a residual covariance. However, a conventional BLUP genetic analysis of a maternal trait such as CE yields a single 'aggregate' residual variance which consists of $\sigma^2_e = \sigma^2_{ed} + \sigma^2_{em} + 2\sigma_{edm}$ where σ^2_{ed} and σ^2_{em} are the variances of the environmental direct and maternal component which contribute to the phenotype (Willham, 1963). The separate components of this 'aggregate' variance are therefore

unknown. In this study, we have fixed both the residual direct variance and the residual maternal variance at the aggregate residual variance used for national genetic evaluations. They are therefore the same. Although this variance will be an overestimate, fitting it as such is common (Mrode et al., 2005). We refer here to all conventional variance based models which incorporate a maternal genetic effect following Willham's model (1963), where the same residual variance is used in the calculation of prediction error variances for both direct and maternal estimated breeding values (Mrode et al., 2001). The residual covariance should thus theoretically equal 0, as

$$\mathbf{R} = \begin{bmatrix} r11 & r12 \\ r21 & r22 \end{bmatrix} = \begin{bmatrix} \sigma^2_{e1} & \sigma_{e12} \\ \sigma_{e21} & \sigma^2_{e2} \end{bmatrix} = \mathbf{I}\,\sigma^2_e \text{ if } \sigma_{e12}=0 \text{ and } \sigma^2_{e1} = \sigma^2_{e2} \qquad [5.6]$$

thereby conforming to the mixed model equations of a conventional BLUP maternal model as described in Chapter 3. Although theoretically correct, the model remains slightly arbitrary as the residual variances that are fitted are overestimates. It is therefore plausible that the prediction of the DRPs for the validation set, and hence the accuracy of DGVs, is suboptimal when this model is fitted. To evaluate if and how sub-optimal the model is under the assumption of a zero residual covariance, we have evaluated prediction by the model when the residual correlation between traits was varied between from -1 to 1 in steps of 0.1.

5.2.2.3. Multiple trait de-regression

PTAs for CEd and CEm follow from conventional BLUP models which accommodate a direct-maternal genetic covariance. De-regression of these PTAs would therefore optimally involve the de-regression of a model that similarly accounts for a genetic relationship between both traits. This can be achieved through

a multiple-trait de-regression. Multiple trait de-regression is probably most widely used in the computation of DRPs to the multiple-trait across country evaluation (MT-MACE) for international bull comparisons (Schaeffer, 2001). Within country *i* and for trait *j* MT-MACE follows the model

$$\mathbf{y}_{ij} = 1\boldsymbol{\mu}_{ij} + \mathbf{Q}\mathbf{g}_{ij} + \mathbf{s}_{ij} + \mathbf{e}_{ij} \quad [5.7]$$

where $\mathbf{y}_{ij}$ is the vector of DRP*s*, $\mathbf{u}_{ij}$ is a overall mean effect, $\mathbf{g}_{ij}$ is the vector of genetic group effects of phantom parents, $\mathbf{s}_{ij}$ is the vector containing random sire proofs and $\mathbf{e}_{ij}$ is the vector of random mean residuals (Mrode, 2005; Schaeffer 2001). **Q** relates sires to phantom parent groups. In this study, we follow this same model but assume just a single country with two traits. Let **K** be a matrix of sire-maternal grandsire covariances and **R** be a matrix of residual covariances, as listed in Table 1. Base animals were assigned phantom parents grouped by the year of birth of their progeny. The DRPs were then obtained by back solving Equation (5.7) for $\mathbf{y}_i$ as described by Schaeffer (2001) using the software MiX99 (Lidauer et al., 2011) which was provided with a full animal pedigree. The difference between univariate and bivariate de-regression is equivalent to the difference between a univariate and bivariate regression of PTAs on phenotypes, as previously described. The right hand side of the mixed model equations for a univariate de-regression equals:

$$\boldsymbol{R}_i^{-1}\boldsymbol{y}_i = \boldsymbol{R}_i^{-1}\mathbf{1}\hat{\boldsymbol{u}}_i + (\boldsymbol{R}_i^{-1} + \boldsymbol{A}_{nn}^{-1}\alpha_i)(\boldsymbol{Q}\hat{\boldsymbol{g}}_i + \boldsymbol{s}_i) + \boldsymbol{A}_{np}^{-1}\hat{\boldsymbol{p}}_i\boldsymbol{\alpha}_i + \boldsymbol{A}_{ng}^{-1}\hat{\boldsymbol{g}}_i\boldsymbol{\alpha}_i \quad [5.8]$$

where $\boldsymbol{R}_i^{-1}$ is the inverse matrix with residual variances where diagonal elements relate to the effective daughter contribution of each bull divided by the residual variance, y_i, and s_i relate to components listed in Equation 5.7, $\hat{\boldsymbol{u}}_i$ is a factor of the overall mean of country *i*, $\hat{\boldsymbol{g}}_i$ is a vector of predicted genetic group effects, $\hat{\boldsymbol{p}}_i$ is a

vector of identified parents without proofs and n, p and g for animals with records, ancestors and genetic group. $\boldsymbol{A}_{xx}^{-1}$ are blocks of the inverse relationship matrix.

This same right hand side in a bivariate de-regression equals

$$\boldsymbol{R}_i^{-1}\boldsymbol{y}_i = \boldsymbol{R}_i^{-1}\boldsymbol{X}\hat{\boldsymbol{u}}_i + \left(\boldsymbol{R}_i^{-1} + \boldsymbol{A}_{nn}^{-1} \otimes \boldsymbol{K}_{ij}^{-1}\right)(\boldsymbol{Q}\hat{\boldsymbol{g}}_i + \boldsymbol{s}_i) +$$

$$(\boldsymbol{A}_{np}^{-1} \otimes \boldsymbol{K}_{ij}^{-1})\hat{\boldsymbol{p}}_i + (\boldsymbol{A}_{ng}^{-1} \otimes \boldsymbol{K}_{ij}^{-1})\hat{\boldsymbol{g}}_i \qquad [5.9]$$

Where components are as in Equation 5.8, **X** is a known incidence matrix relating records to traits and $\boldsymbol{K}_{\boldsymbol{ij}}^{-\mathbf{1}}$ is a two by two inverse additive genetic variance covariance matrix among the *j* traits in country *i*. Hence, scaling in the multi-trait de-regression is consistent with the scaling performed by a conventional maternal BLUP model when estimating PTA's (Mrode, 2005).

5.2.2.3.1 Multi-trait effective daughter contributions

In de-regression, DRPs are weighted by the effective daughter contribution which accounts for the differences in precision of daughter information contributing to the DRP for each bull. The effective daughter contribution is a function of the reliability of each source of progeny information and a constant *k* which refers to the computation of the diagonal element of the coefficient matrix (Mrode et al., 2005).

The equation to compute EDC, including the performance of the dam of daughter *n* of bull *i* was described by Fikse and Banos (2001) as

$$EDC_i = \sum \frac{k * rel_{k(0)}}{4 - rel_{k(o)}(1 + rel_{dam(o)})} \quad , \qquad [5.10]$$

where the summation is over all n daughters of bull *i*, k=(4-h^2)/h^2, h^2 being the heritability, $rel_{k(o)}$ is the reliability of the animal n's own performance and $rel_{dam(o)}$ is the reliability of the dam's own performance. Due to the genetic correlation between direct and maternal effects in CE, the original single trait computation of EDCs, is no

longer applicable. This makes sense as reliabilities for PTAs of bulls are different for a model which account for a genetic variance-covariance structure and *k* adjusts accordingly. The computation of multiple trait EDCs for a model with correlated direct and maternal genetic effects was described by Liu et al. (2003). Like the single trait EDC, it involves the summation of progeny contribution for each bull. The difference is that in the case of direct and maternal effects, data information contributing to the reliability of records for *n* offspring can be added through records on CEd (being born), CEm (giving birth), or both CEd and CEm.

Thus, progeny information is needed for the computation of multiple trait EDCs. For this study, genotypes of bulls originated from several countries and the required progeny information was not available. To still allow a multiple trait de-regression, we used ratios of single trait EDCs to multiple trait EDCs per year of birth as provided by Liu et al. (2003) to approach multiple-trait EDCs. Ratios were reported by Liu et al. for varying genetic direct-maternal correlations. We therefore computed ratios concurrent to our genetic correlation by plotting the ratio's provided by Liu et al. within year of birth, and equating the resulting quadratic function to our genetic correlation of -0.57. Subsequently, each ratio was plotted per year of birth and a trend line was fitted such that EDCs could be approximated for years of birth not analysed in Liu et al. (2003). Trend lines were assessed on goodness of fit of the trend line by R^2 which showed highest values for a polynomial trend line in both CEd and CEm. The order of the polynomials was further assessed by cross-validation to consider predictive problems resulting from overfitting. A polynomial of the 3rd order proved to best fit the ratios for both CEd and CEm and R^2 of each fit equalled 0.94 and 0.90 respectively. DRPs for CEd and CEm obtained by the multi-trait de-

regression weighted by the multi-trait EDCs were subsequently used as dependent variables in the univariate (MDSTgBLUP) and bivariate (MDMTgBLUP) gBLUP models.

5.3. Results

5.3.1. Accuracies

5.3.1.1. Multi-trait models

The accuracy of DGVs for CEm increase when estimated by the MTgBLUP model compared to the STgBLUP model (Table 5.2). The relatively small increase however implies that added value of the MTgBLUP model to increase accuracy is limited. Accuracy of DGVs for CEd is unaffected by the fitting of the MTgBLUP model. Regression of DGVs on DRPs indicates that the STgBLUP model overestimates the variance of CEm DGVs ($b_{DGV,DRP}$=1.07). The MTgBLUP model appears to predict DGVs for CEm slightly better as the regression coefficient reduces to 1.06. This implies that overestimation of the variance for CEm can be reduced by simply allowing for a genetic covariance in a multi-trait gBLUP model even when proofs are univariately de-regressed. The STgBLUP model underestimates the variance of CEd DGVs ($b_{DGV,DRP}$=0.89). The MTgBLUP model shows a slight increase in this underestimation. This is likely due to the phenomenon shown by Figure 5.1. In all gBLUP models the residual covariance is fixed to 0 which for CEd is not the value at which the highest accuracy of DGV is achieved (which is at a residual correlation of -0.6) when DRPs for CEd are univariately de-regressed. This will be discussed further on in the Chapter.

5.3.1.1.1. Multi-trait de-regression

Deregressing proofs for CEd and CEm by a multi-trait de-regression model and thereby accounting for a direct-maternal genetic covariance shows to have a positive effect on the accuracy of DGVs for CEm. Regardless if the multi-trait DRPs are fitted to a single trait or a multi-trait gBLUP model, predictive ability of DGVs for CEm improves considerably by the multiple-trait de-regression ($b_{DGV,DRP}$=0.99). Accuracies of DGVs for CEm are highest when the DRPs are estimated through multiple-trait de-regression and subsequently fitted in a bivariate gBLUP model (MDMTgBLUP). In contrast, accuracy of DGVs for CEd remains unaffected by the multiple-trait de-regression but predictive ability of the model is decreased.

Table 5.2 Accuracies and reliabilities of DGVs obtained by four different gBLUP models

Trait	CEd			CEm		
Model[1]	$r_{DRP,DGV}$	$r^2_{DRP,DGV}$	$b_{DGV,DRP}$	$r_{DRP,DGV}$	$r^2_{DRP,DGV}$	$b_{DGV,DRP}$
STgBLUP	0.56	0.31	0.89	0.57	0.32	1.07
MTgBLUP	0.56	0.31	0.88	0.58	0.33	1.06
MDSTgBLUP	0.55	0.30	0.86	0.58	0.33	0.99
MDMTgBLUP	0.56	0.31	0.86	0.59	0.35	0.99

5.3.2. Residual covariance

Figure 5.1 shows that the highest accuracy of DGVs for both CEd and CEm were achieved with a residual covariance < 0 when DRPs were de-regressed univariately. The highest correlation between DGVs and DRPs was achieved for CEd and CEm respectively when the residual correlation equalled -0.6 and -0.2, implying that the prediction of DGVs for CEd is most affected by the suboptimal fit of the model.

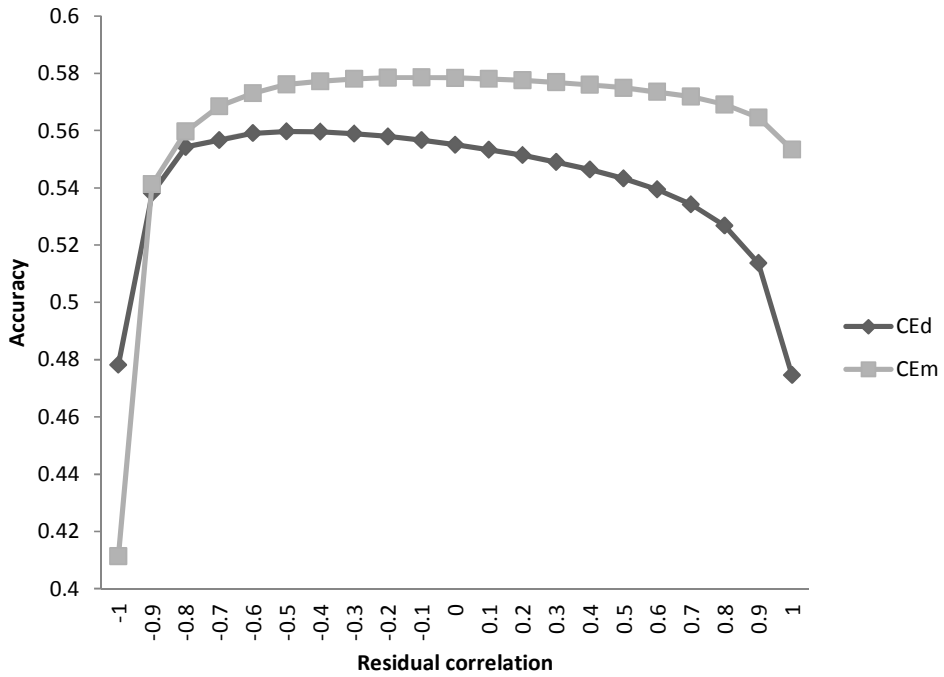


Figure 5.1 The accuracies of direct and maternal DGVs obtained from bivariate gBLUP models fitting univariate de-regressed sire proofs and a varying residual covariance (for the x-axis these covariances are transformed into correlations).

5.4. Discussion

We evaluated two potential ways to improve estimation of DGVs for CEd and CEm. We first extended the current single trait genomic model (STgBLUP) for direct and maternal CE to a multi-trait gBLUP model (MTgBLUP) and then adapted the single trait de-regression of PTAs for CE to a multi-trait degression. The multi-trait de-regressed DRPs for CEd and CEm were subsequently fitted as surrogate phenotypes in the univariate (MDSTgBLUP) and bivariate (MDMTgBLUP) models. Multiple-trait EDCs were approached through scaling factors adapted from Liu et al. (2003). Correlations between estimated DGVs and DRPs of a validation population served as accuracies. Furthermore, a regression coefficient of DGVs on DRPs was calculated

to represent the predictive ability of the model. By finding increases of accuracy from fitting a multi-trait genomic model we confirm findings by Calus et al. 2010 and VanRaden et al. 2010 who report the advantages of multi-trait genomic evaluation. The relatively small increase is supported through simulation by Calus et al. 2011 where a MT model is compared to a ST model assuming a comparable genetic correlation of -0.54. Findings of this study show added value in multi-trait genomic models for the application to CE as predictive ability of DGVs for CEm improved by accounting for the genetic make-up of a maternal trait, as conventional BLUP models. Advantages of the multi-trait genomic model are however limited to CEm as the estimation of DGVs for CEd were unaffected and the predictive ability of the model decreased slightly.

To our knowledge, we are the first to attempt a multi-trait genomic model for calving ease. Furthermore, there is no report of the application of a multiple-trait de-regression for the purpose of using subsequent DRPs for the prediction of DGVs. However, theoretically, the increase of accuracy and predictive ability of the MDMTgBLUP model can be rationalised as this model approaches the conventional model which estimated the PTAs closest by consistently accounting for the genetic relationship between CEd and CEm. It must be noted however that in doing so, a large assumption was made when computing multiple-trait EDCs. To confirm the positive results of this study with regards to a multiple-trait de-regression, multiple trait EDCs should be computed from exact progeny information and analyses should be repeated. By doing so, the decrease of predictive ability for DGVs of CEd can also either by confirmed or rejected as an artefact of the approach used to compute EDCs in this study. Nevertheless, this study gives incentives for the further

exploration of multiple de-regression and shows potential benefit in accounting for the direct-maternal genetic covariance at both de-regression of DRPs and re-regression of DGVs on DRPs. Additional future improvement of the genomic model for CE in the UK can likely be achieved through the addition of a polygenic effect which would account for any variance not explained by markers (Mrode et al., 2012).

5.4.1. Evaluating potential bias of the genomic model due to the residual variance/covariance matrix

Figure 5.1 shows that accuracies of DGVs for CEd and CEm were higher when the residual covariance fitted between traits deviated from its theoretical correct value of 0. This deviation of 0 is likely an artefact of the model caused by the introduction of a direct-maternal genetic covariance. The covariance between DRPs of CEd and CEm equals

$$Cov(DRP_{CEd}, DRP_{CEm}) = Cov(DGV_{CEd} + E_{CEd}, DGV_{CEm} + E_{CEm})$$

$$= \sigma_{DGV_{CEd},DGV_{CEm}} + \sigma_{E_{CEd},E_{CEm}} \quad , \quad [5.11]$$

assuming no covariance between genetics and environment. DRPs were de-regressed univariately thus the direct-maternal genetic covariance was assumed to be 0. By fitting the MTgBLUP model, a direct-maternal genetic covariance was introduced. Hence, Equation [5.11] is only mathematically correct when the residual covariance accordingly adjusts, as the covariance between DRPs is fixed. The genetic direct-maternal correlation is negative, which can be seen in Table 5.1, and thus the adjustment of the residual covariance is downwards. The difference in adjustments between CEd and CEm (CEd:-0.6, CEm:-0.2) results from the residual variance being an aggregate variance. By detecting a difference, we can imply that the two underlying residual variances are not equal. By performing a multiple-trait de-

regression, we have accounted for the genetic direct-maternal covariance at de-regression. It is therefore expected that when varying the residual covariance once again, highest accuracies are found at less severe deviations from 0. Figure 5.2 shows the results from this analysis and confirms our expectation, which also explains partly the benefit in predictive ability of DGVs for CEm by the MDMTgBLUP model. Highest accuracies are now found at a residual correlation of -0.4 for CEd and +0.2 for CEm. A deviation from the theoretically correct value of 0 is however still present. This is a direct result from the suboptimal fit of the model due to the aggregate residual variance. As the residual variance fitted per trait is an overestimate of the actual residual variance the model expects, the varying residual covariance will show best predictions at values related to bias of the aggregate residual variance in relation to the true residual direct or maternal variance.

From information given by Figure 5.2 we can however approximate what the separate direct and maternal residual variances may be, given that the aggregate residual variance equals 0.429 and given that we have varied the residual correlation by steps of 0.1. From Figure 5.2, we can determine that the aggregate residual variance overestimates the direct residual variance by an amount equal to the aggregate residual covariance related to the residual correlation of -0.4 and underestimates the maternal residual variance by an amount equal to the aggregate residual covariance related to the residual correlation of 0.2. Knowing that the aggregate residual variance consists of $\sigma^2_{ed} + \sigma^2_{em} + 2\sigma_{edm}$ the direct-maternal residual covariance can be derived. We have repeated the MDgBLUP model fitting the now more accurate residual variance-covariance matrix. Accuracy of DGVs for CEd increased to 0.58 and accuracy of DGVs for CEm reached 0.62. It must

however be noted that fitted EDCs were still functions of reliabilities which are estimated by conventional BLUP models, hence using aggregate residual variances. This inconsistency resulted in a decrease of predictive ability for both CEd and CEm. It can however clearly be concluded from Figures 5.1 and 5.2 that multiple de-regression contributes to a better prediction of DGVs for CEd and CEm.

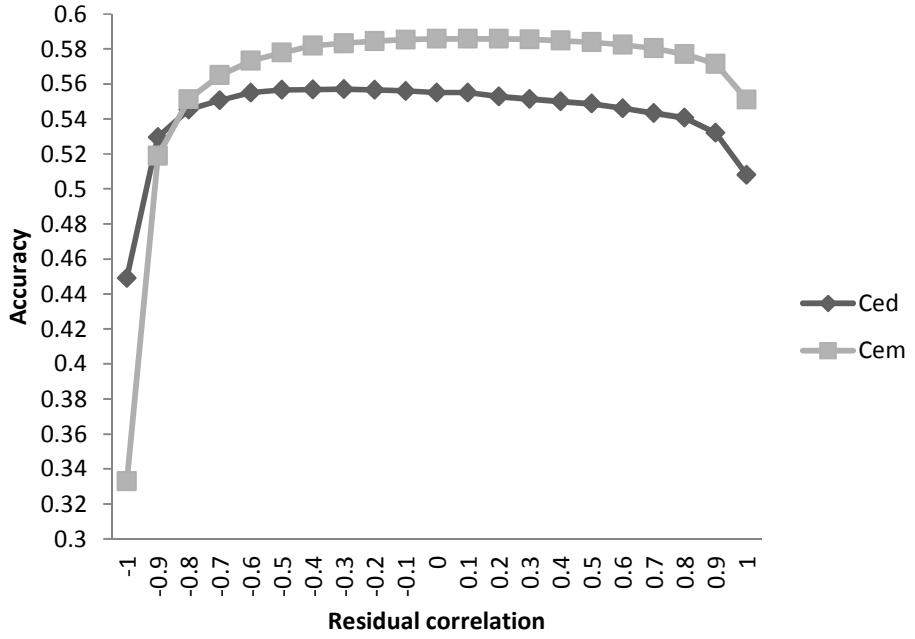


Figure 5.2 The accuracies of direct and maternal DGVs obtained from bivariate gBLUP models fitting multivariate de-regressed sire proofs and a varying residual covariance (for the x-axis these covariances are transformed into correlations).

5.5. Conclusions

The genomic prediction of DGVs for CE benefits from a careful consideration of the traits' genetic make-up. Gains in the predictive ability and the accuracy of DGVs were obtained by accounting for a genetic direct-maternal covariance through the fitting of a bivariate gBLUP model. Further gains were obtained by also accounting for this genetic relationship at de-regression. Computation of necessary multiple-trait

EDCs was, however, achieved through scaling and analyses should be repeated through exact computation. By varying the residual covariance between traits, thereby evaluating the potential bias of the genomic model by its theoretically correct assumptions, showed that maternal traits like CE cannot be evaluated by genomic models which were designed to fit non-maternal traits. Even after accounting for a genetic direct-maternal covariance and taking into account the complex genetic make-up of the maternal trait, accuracies of predictions are hampered by the aggregate residual variances that are estimated through conventional BLUP models. Accuracy of DGVs for CE can therefore be improved by acknowledgement of the trait's characteristics when designing a genomic prediction model for CE.

CHAPTER 6:

General discussion and conclusion

6.1 General discussion

When there is genetic variation, a trait can respond to genetic selection. However, in what direction the trait will change and how much genetic progress can be made is a different issue. Genetic selection in dairy cattle crudely follows five major steps

i. Data recording
ii. Evaluation of models + estimation of genetic parameters and breeding values
iii. Communication of proofs to clients of the genetic evaluation service
iv. Dissemination of semen to farmers + communication of proofs to farmers
v. Selection of sires and insemination of cows by farmers

Each step in itself has the potential to hamper the amount of genetic progress that is ultimately realised in practice. Scientists primarily influence step ii. The remaining steps are highly dependent on interaction between researchers, industry and farmers. The flow of genetic selection in the UK e.g. from data recording to communication of proofs to farmer, is pictorially described by Figure 6.1.

Relative to a trait such as milk production, genetic selection on calving traits faces large challenges in each of the four steps described above. This inevitably slows down genetic progress. In this thesis, some of these challenges were revealed (Chapter 2, 3, 4), faced (Chapter 3, 4) and addressed (Chapter 3, 4, 5). This general discussion serves to evaluate the deductions from this thesis on how to maximize genetic progress and discuss what challenges still lay ahead.

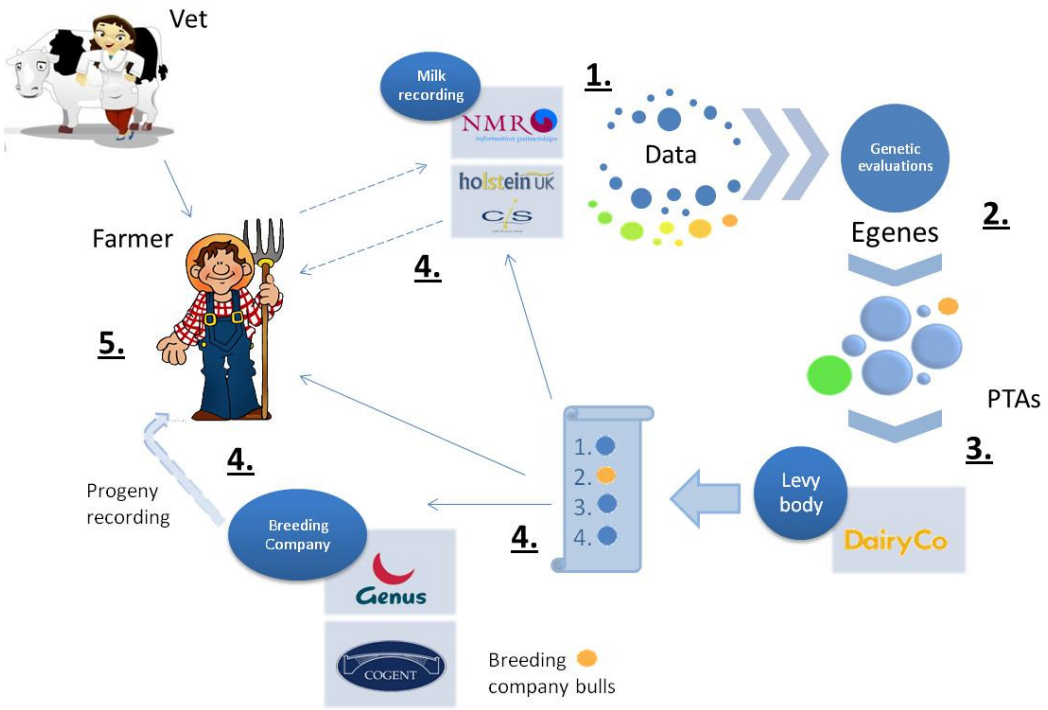


Figure 6.1 Pictorial description of the genetic evaluation and selection flow in UK dairy cattle

6.1.1. Summary of thesis objectives

Successful calvings are fundamental for the sustainability of a dairy cattle farm as consequences of poor calving performance have large economic and animal welfare implications (McGuire et al., 1998, Barrier et al., 2011, 2012; this thesis). Yet, currently almost 1 in 5 Holstein-Friesian calvings in the UK are associated with some degree of difficulty, ranging from the need for farmer assistance to the need for veterinary assistance. Decreasing the incidence of calving complications would therefore be highly beneficial to the UK dairy cattle industry and genetic selection is a potential tool in the reduction of calving complications. However, the complex phenotypic make-up of calving traits complicates genetic evaluations.

The general goal of this thesis was to evaluate how genetic selection on calving traits can be implemented in the UK. Emphasis has been put on the gains of improvement

in calving performance and how a range of genetic parameters can be best estimated. This general goal has been split up in to four straightforward objectives that are each represented by a question

1) To what extent do difficult calvings affect the performance of a dairy cattle herd?
2) How can we 'best' evaluate genetic parameters for calving traits?
3) How are calving traits genetically related to other important (selection) traits in dairy cattle breeding?
4) Can the current genomic prediction model for calving ease be improved to increase accuracies of estimated genomic breeding values?

6.1.2. Deductions from the study

6.1.2.1 Time does not heal all wounds

The prevalence of difficult calvings and stillbirths in the UK, as reported in Chapter 3 and 4 shows that there is no doubt that UK Holstein-Friesian dairy cattle experience calving complications. Approximately 21% of all cows have been given assistance of some sort at their parturition and 6% of all calves are stillborn. Awareness of the problem is essential for the success of genetic selection. Farmers need to have an incentive to start selecting for easy parturitions, and this will come from evidence of a detrimental effect on the profitability of the herd, perhaps alongside the ethical benefit of improving animal welfare. Extensive research by animal behaviourists had already shown that a difficult calving impacts negatively upon the subsequent performance of the dam and this was confirmed by findings in this thesis (Chapter 2). Immediate economic effects of a difficult calving are

therefore established. Chapter 3 however also reveals that there is an association between a difficult calving and the subsequent performance of the *calf* two years after birth, as an adult member of the dairy cattle herd. Milk production of heifers which were veterinary assisted at birth, compared to heifers which were unassisted at birth showed a considerable difference of -703 kg per 305-day lactation.

This first indication that difficult calvings do not only affect the health and vitality of the dairy calf but actually have an impact upon the long term profitable farming enterprise should bring more attention from the dairy cattle industry to the consequences of perinatal complications on the life and performance of a dairy calf. It has to be stressed however that this is one of only two studies which searches for an association between a difficult birth and subsequent adult performance. Although the results support each other, it is key that further research is conducted to confirm this relationship. Ideally, calving performance prior to the lactation which is linked to the difficult birth of the individual would be recorded and corrected for. It also has to be emphasised that this finding shows an association between direct calving ease and milk production, not a cause-and-effect relationship. We can therefore not state that the difficult birth is the cause of the relatively low milk production. It is equally possible that there is a third factor mediating both traits. What we *can* say is that Chapter 5 reveals a genetic correlation between direct calving ease and milk production which might underlie the phenotypic association that has been identified. In addition, the emerging fields of developmental programming and epigenetics gives scope for further research on what underlies this association. The research community should not shy away from more advanced research on the relationship

between foetal conditions and subsequent behaviour/performance in other mammals, including humans (O'Callaghan et al., 1992)

6.1.2.2. Parameters and strategies for genetic selection

6.1.2.2.1. The genetic model

Both in Chapter 3 and 4 it has been shown that there is genetic variation in calving ease and stillbirth in the UK. In other words, genetic selection is possible although heritabilities are low and therefore genetic progress will be relatively slow.

A wide range of models for the estimation of genetic parameters for calving ease and stillbirth were analysed in this thesis. Of all these models, a multi-trait sire-mgs model was recommended for the estimation of genetic parameters considering both accuracy and practicality. Sire-mgs models proved to be robust when models were made more complex by the addition of extra traits. These additional traits were shown to benefit the accuracy of estimated proofs, and so this favours the use of the sire-mgs model. However, it could be that, for national genetic evaluation, the animal model is preferred over the sire-mgs model due to its ability to estimate proofs for cows as well as sires. Work in this thesis shows that animal models are computationally limited to bivariate traits with two random effects. Achieving convergence to sensible results with anything more complex would prove very difficult. Animal models required considerably more computing time than sire-mgs models. However, even sire-mgs models with more than one maternal trait needed weeks rather than days to reach convergence. Trivariate animal and sire-mgs models, fitting all three maternal traits (calving ease, stillbirth and gestation length) in one model were attempted but failed to converge. A change of software package was tested to see if it would reduce computational time by comparing ASReml (Gilmour

et al., 2006) to VCE (Groeneveld et al., 1990). Speed of convergence was however similar. Furthermore, it was explored if Gibbs Sampling would decrease the computational time (by avoiding the need to solve many mixed model equations) by a Markov Chain Monte Carlo sampling approach (Van Tassell et al., 1995). However, it turned out that the chosen statistical software package, DMU v6.0 (Jensen and Madsen, 2010) has yet to accommodate maternal models. ASReml therefore remained the variance component estimator of choice. It would be wise to keep updated on future developments in software packages for animal breeding.

The parameters that were estimated in this thesis serve to facilitate the uptake of genetic selection for calving ease in the UK. By choice, all analyses were conducted with a linear mixed model which has the large advantage of ease of implementation. Hence, programs used in national genetic evaluation can be used without modification. However, alternative statistical models that have been suggested for the analyses of calving traits, such as structural equation models (De Maturana et al., 2007) and threshold models or linear-threshold models (Varona et al., 1999) have not been considered. Structural equation models of the recursive type as used by Maturana et al. (2008) may give further insight into biological relationships between calving ease, stillbirth and gestation length as the existence of recursive relationships between these traits is very plausible. They have however only recently been adopted by animal breeding (De Los Campos, 2006a) and are rarely used for parameter estimation, possibly due to their considerably higher complexity and computational demand (De Maturana et al., 2008). As explained in Chapter 4, evidence of the practical advantage of threshold models over linear models for the analyses of calving ease is still low (Meijering and Gianola, 1985; Clutter et al., 1988; Weller et

al., 1988; Lee et al., 2002). It is therefore reasonable to expect little to no differences in the ability to elicit larger response to selection when the threshold model is used for parameter estimation instead of the linear model. Yet, this can only be confirmed when analyses are repeated by consideration of both the threshold model and the method used to fit it e.g. Bayesian methodologies (Chapter 3). Considering its binary nature, advantages of the threshold model may be larger for stillbirth which is worth investigating (Meijering and Gianola, 1985).

6.1.2.2.2. The genomic model

Chapter 5 addresses the improvement that can be made to the genomic model for calving ease in the UK. As proofs were only available for calving ease, a similar study could not be conducted for stillbirth. Yet, many of the issues that are addressed in Chapter 6 relate to maternal traits in general and methods could therefore be generalised. Considering Chapter 3, there is however currently too much noise in the estimation of variance components for stillbirth to attempt a genomic multi-trait model for stillbirth.

The main conclusion from Chapter 5 is that accuracies of genomic proofs can be increased by taking account of the maternal character of the calving trait. In other words, by assuming direct and maternal calving ease to be independent when we know from conventional genetic analyses (Chapter 3) that they are not, the accuracy of proofs is negatively affected. Additionally, care is needed in the de-regression of proofs for maternal traits as a multi-trait de-regression is needed and the weights e.g. effective daughter contributions then differ from single-trait weights. Multi-trait de-regression with single-trait weights results in an increase in the variance of de-regressed proofs, and subsequently a considerable decrease in accuracy of genomic

proofs. Currently, much attention is given to procedures for single-step genomic evaluations which combine full pedigree and genomic evaluation by the ability to evaluate a mix of phenotypic and genomic data (Misztal et al., 2009; Meuwissen et al., 2011). Although this would solve many of the statistical complexities that are addressed in Chapter 6, it would only do so when reference populations are built within countries and hence actual phenotypes for calving ease can be fitted as data. When reference populations are built from collaboration between countries, such as the one used in the UK referred to in Chapter 6, and the surrogate phenotype of choice is the de-regressed national or international proof on a national scale then problems related to the genetic and environmental relationship between direct and maternal calving ease remain and need to be dealt with.

In January 2012, genomic proofs for direct and maternal calving ease were published. Considering Chapter 5, it would be advisable to perform a multi-trait de-regression with accurately calculated weights and subsequently extend the genomic model to a multi-trait model to estimate the genomic proofs for future publications.

6.1.2.2.3 What can be improved?

Stillbirth

A full genetic evaluation for the trait of stillbirth proved to be difficult. A large proportion of the analyses conducted in Chapter 3 and 4 were attempted yet not successful for stillbirth. This is partly due to the complex nature of the trait. Stillbirth is a binary maternal trait with low incidence, and low genetic variances. Thus, little information is available for the separation of many variance components. Difficulty of estimation shows in the estimates of the direct-maternal genetic correlation which are accompanied by very high standard errors and are sensitive to model structure

(Chapter 3). When models become more complex and the separation of more variance components is needed, such as the between parity models in Chapter 4, or the trivariate models in Chapter 5, analyses for stillbirth failed to converge as likelihood surfaces became too flat to provide a maximum likelihood estimate. Sire models had less problems in reaching convergence for analyses involving stillbirth than animal models as relatively more information is available per sire than per animal. Nevertheless, sire-mgs models for stillbirth consisting of more than two traits or more than two random genetic effects failed to reach convergence. Failure to estimate the genetic relationships between stillbirth and traits in the national genetic index hampers the inclusion of stillbirth in the national breeding goal which will have considerable limitations to the realised genetic progress in this trait. The problematic analyses of stillbirth, however, can be considerably improved by improvement of the data quality. Many records on stillbirth in the dataset available for this thesis did not contribute information due to the sex of the stillborn calf being unrecorded. Due to the nature of the trait, a large quantity of data is needed in order to estimate sensible genetic parameters. Increasing good quality data on stillbirth is therefore one of the strongest recommendations arising from this thesis. This will also benefit genomic evaluations on stillbirth which are likely to develop in the near future considering the fast implementation of genomic selection in dairy cattle breeding worldwide.

Indicator traits

Gestation length was chosen to serve as an indicator trait in order to enhance estimation of genetic parameters for calving ease and stillbirth. Gestation length was suggested to be genetically correlated to calving traits (Maturana et al., 2008; Van Pelt et al., 2009) and is known to be moderately heritable. With good data on

gestation length provided, it was an easy candidate to evaluate the value of indicator traits. Gestation length was shown to be moderately correlated to calving ease and stillbirth (Chapter 3). The value of gestation length as an indicator trait is therefore still open for discussion although the predictive ability of the model benefitted from the inclusion of a highly heritable trait (Chapter 3).

In the literature, genetic correlations of calving ease and stillbirth are often higher than those with gestation length (Hansen et al., 2004). This would be expected as the inclusion of birth weight as a correlated trait to the model with calving ease and/or stillbirth would benefit estimation of genetic parameters. Unfortunately, birth weight is currently recorded only in a fashion that is highly subjective, on a three class scale according to size of the calf e.g. 1. small – 3. large. It was therefore chosen not to include birth weight in any analyses conducted in this thesis work. It is a strong recommendation to the industry to develop a less subjective method of recording of birth weight. One suggestion might be to develop a scoring scale similar to that used in The Netherlands where grades refer to actual weight instead of size. A 12 grade scale could be used where grade 1 refers to calves <25kg and each grade subsequently represents a step of 5kg. Hence, grade 2 equals calves 25-30 kg, etc. Even when farmers or technical staff do not have the ability to actually weigh the calf and must approximate the weight, this scale based on weights is still expected to reduce the current between herd variation in scores as scale units (kilogram vs. size) are less subjective.

6.1.2.3 Calving ease in PLI

In this thesis, we evaluate the potential for genetic selection to aid in the reduction of difficult calvings. This would be beneficial as it would decrease costs and increase

animal welfare. Nationally, we aim to improve multiple traits simultaneously and, as the national breeding program is economically orientated, we aim to improve these traits with the breeding objective of maximising economic merit. Information on several traits, that are not necessarily the same traits as in the objective, is accumulated to form the national genetic index (PLI in the UK, as described in Chapter 1) which provides the selection strategy to achieve this breeding objective.

Calving traits are shown to be of considerable economic importance to the dairy cattle industry (McGuirk, 1998; this thesis). It would therefore be a logical step to use the information gathered in Chapter 4 to include calving ease in the national breeding objective and the national genetic index in order to improve the trait through improvement of total economic merit. From selection index theory and the genetic parameters estimated in Chapter 4 we can therefore answer questions which arise logically from the work done in this thesis:

1. What is the response of direct and maternal calving ease to selection on the current PLI?
2. What is the genetic response of direct and maternal calving ease when they are included in PLI ?

6.1.2.3.1. Calculation of economic weights

The following section on the calculation of economic weights for direct and maternal calving ease is partly adapted from the work of Peter Amer from AcacusBIO for SAC (Amer et al., 2009)

To be able to calculate the optimal index for maximizing profit each trait that contributes to the breeding objective is assigned an economic weight. This weight represents the return in £ of 1 unit change (improvement) in the specific trait per

animal. Thus, to include calving ease in the breeding objective, we need to calculate its relative economic weight. As there are two genetic traits that contribute to calving ease, direct calving ease (ease of birth) and maternal calving ease (ease of calving) we will need to calculate two separate economic weights.

The economic weight of direct and maternal calving ease can be calculated by listing the costs and revenues of each trait. In the case of calving ease, there are no revenues so we only have to list the costs. The costs of direct and maternal calving ease separately can be deduced by evaluating where a sire's genetic merit for each trait is expressed and what costs this expression subsequently brings about (costs are likely to differ between sexes as time of expression will differ between sexes but here we will limit ourselves to sires).

As a result of one successful insemination genes for both direct and maternal calving ease are transferred to descendants, as also discussed in Chapter 3. Half of the sires genes for direct calving ease is expressed when each of its calves is born. Assuming a standard dairy cattle situation, presented by Figure 6.2, heifer calves would likely be kept on the farm to serve as heifer replacements whereas bull calves would be removed as surplus. When the daughter of the sire is kept as a replacement heifer and calves, ½ of the sire's genes for maternal calving ease + ¼ of the sire's genes for direct calving ease are expressed in the sire's grand offspring. This happens repeatedly with every calving of the sire's daughter.

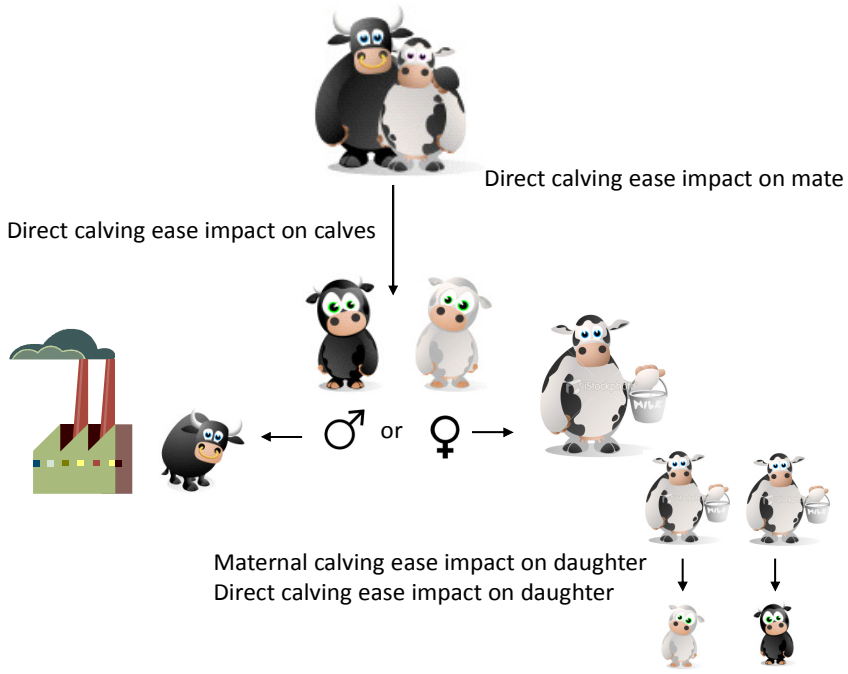


Figure 6.2. Short term impact of sire's genes for direct and maternal calving ease following a successful insemination

Now we have listed the expressions, we can evaluate the effects of expression. If the expression of the sire's genes for direct calving ease in his calf will cause a difficult calving this will bring about labour and veterinary costs. Furthermore, as we have seen in Chapter 2, the difficult birth can cause reduced performance of the calf which is a loss in revenue. However, consistent reduced performance by the sire's daughters will feed into the estimation of the sire's PTA for these traits, such as milk production. The costs associated with reduced performance of the daughters are therefore largely picked up by the affected traits also in PLI and are not counted again. The difficult calving as a result of the sire's genes for direct calving ease, however, can also cause a reduced performance of the mate which would not be accounted for in the bulls PTA unless the calf were inbred. These costs should therefore be assigned to direct calving ease:

- Costs associated with direct calving ease: labour and veterinary costs of the calving + reduced performance of the mate

The sire's genes for maternal calving ease come to expression when his daughters calve. Reduced performance again feeds back into the sire's PTA estimation and thus only labour and veterinary costs of this calving have to be listed.

- Costs associated with maternal calving ease: labour and veterinary costs

Now that costs are listed, we need to multiply the sum of the costs by a discount factor. This is used to turn the future costs into the value of the costs at the time of the successful insemination in year zero. The discount factor is dependent on the discount rate, which is essentially the interest rate it will take to turn today's money into tomorrow's value (but calculated in the other direction) and on the time and frequency of expression of the sire's genotype. Time horizon determines how strongly costs need to be discounted. As direct and maternal effects are expressed at different moments in time, the discount factors will differ for direct and maternal calving ease. Maternal calving ease is expressed much later in time, thus it is expected to be discounted stronger.

To work out the discount factors, we first count the number of possible expressions of a sire's genotype resulting from a successful insemination. This can be done through gene flow procedures in which the growth of number of descendants from an individual over time is traced and numbers of expressions can be counted (Amer et al., 1999; Woolliams et al., 1999). For the specific case of calving ease this is very nicely explained by Balcerzak et al. (1989) and Wolfová et al. (2003). It should be noted that the repeated expressions of the maternal calving ease, as discussed in Chapter 3 are thus accounted for in the discount factor. When having counted the

number of genetic expressions we can then obtain the equivalent number of discounted expressions by adjusting for:

i. the dilution of the sire's genotype (½ in generation i, ¼ in generation i+1);

ii. The probability that each expression actually occurs which depends on the assumed number of lactations per cow and the fact that maternal calving ease is only expressed by females (Balcerzak et al. 1989).

iii. The time that has passed from insemination to each expression. The returns in year *i* should be discounted back to present values by multiplying by the discount rate: (1/1+r) where r is the rate of interest

Discounted expressions can then be summed over an assumed investment period and assumed number of generations. This cumulative number of discounted expressions is called the discount factor and subsequently gets multiplied to the total sum of costs assigned to direct and maternal calving ease respectively, as previously calculated, to end up with economic weights.

- Economic weight for direct calving ease =
  - Discount factor direct * (costs of reduced performance + labour and veterinary costs when calf is born + labour and veterinary costs when grand offspring is born through daughter)
- Economic weight for maternal calving ease =
  - Discount factor maternal * (labour and veterinary costs when daughters calve)

The unit of the economic weights is 1% reduction in severe or worse calvings per cow per lactation. The calculated economic weights were £2.43 for direct calving ease and £1.20 for maternal calving ease

6.1.2.3.2. Selection index calculations

The response of calving ease to selection on PLI when the trait is or is not included in the index can be calculated using selection index theory. Traits in the breeding objective are generally traits of economic importance while the traits in the selection criterion, or index, serve as information sources to deliver the selection strategy for maximising economic merit. To answer the questions in the introduction of this section I have initially evaluated the response of direct and maternal calving ease in two situations.

1. Direct and maternal calving ease are not in the index nor the breeding objective
2. Direct and maternal calving ease are in the in the index and breeding objective

For the calculations I have used parameters provided by the report of the Expanding Indices project to which a large part of this thesis work contributed. As such, the source of information was assumed to be 75 daughter records for each trait, and the selection intensity was 1.346 corresponding to a 'typical' four pathway dairy cattle breeding scheme (Roberston and Rendel, 1950). Generation intervals were assumed to be 6.5 years for sires and 5 years for dams. Genetic parameters were collated through work in this thesis (Chapter 4), further work by the Expanding Indices project and previously reported parameters by Stott et al. (2005) and Wall et al. (2003).

Default traits in the breeding objective and selection criterion were:

- Breeding objective:

milk, fat, protein, calving interval, non-return at day 56 in milk, lifespan, lameness and mastitis (8 traits)

- Selection criterion:

milk, fat, protein, calving interval, non-return at day 56 in milk, lifespan, legs and feet, somatic cell count, mammary composition (9 traits)

Selection index coefficients (b) were calculated following standard selection index theory as

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}\mathbf{v} \quad [6.1]$$

Where P is the matrix of (co)variances between information sources, G is a matrix of (co)variances between the index sources and true breeding values for traits in the breeding objective and v is a vector of economic weights assigned to traits in the breeding objective. Variance of the index was calculated as

$$\sigma_I^2 = \mathbf{b}'\mathbf{P}\mathbf{b} \quad [6.2]$$

and responses in individual traits to selection on the index were computed as

$$\mathbf{R}_g = i\mathbf{b}'\mathbf{G}/\sigma_I \quad [6.3]$$

where R_g is a vector of responses in traits in the breeding objective. For correlated response on a trait *not* in the index G is a vector of genetic covariances between information sources for each trait in the index and the true breeding value for the specific trait not included in the index. All matrices were checked for positive eigenvalues and if needed bended to be positive definite by the software package R v2.12.2 (Venables et al., 2011).

Responses in direct and maternal calving ease are presented in Table 6.1. Responses are expressed in the unit of the trait, which is on the underlying liability scale and in the unit of the economic value e.g. the incidence scale.

Response on calving ease to the current PLI, which disregards the trait, is undesirable although we see a favourable response in maternal calving ease. Subsequent inclusion of calving ease in the genetic index and breeding objective reduces the negative response in direct calving ease however to a small cost in maternal calving ease. The antagonistic genetic relationship between direct and maternal calving ease (Chapter 3) hampers the genetic response in maternal calving ease and as the economic weight for this trait is considerably lower than that of direct calving ease, economic merit is maximised by compromising on the response of maternal calving. Table 6.2 shows the possible responses when this genetic correlation would have been more moderate which might be interesting considering its sensitivity to estimation error as described in Chapter 3.

As response to selection on PLI without calving ease did not show a negative effect on maternal calving ease, a situation was evaluated where only direct calving ease is included in the index and breeding objective. This selection index showed a slightly better response in maternal calving ease although this comes at a cost for the overall economic response of the total breeding objective. It is possible to constrain the response in direct calving ease to zero; hence the decline in response would be stopped. Response in maternal calving ease is then considerably compromised but is still positive. The decision for a restricted index might be justified through the considerable decrease in incidence of direct calving ease. This last, most extreme index, however also compromises the greatest on the overall economic response of the breeding objective.

Whether or not to include calving ease in the national genetic index therefore changes according to priority or desire. If we want to improve the national breeding

objective of maximising economic merit, the best strategy is to include both direct and maternal calving ease in the index and breeding objective. However for improvement of calving ease as a trait, and thus improvement of animal welfare, it is best to only put direct calving ease in the index and objective and constrain its response to zero. In other words, improved animal welfare comes at a cost and in the case of calving ease, this cost is approximately £0.02 per liter of milk produced.

Table 6.1 Response of selection for calving ease on different index selection strategies per generation

Trait[1]	CEd		CEm		
Situation	Underlying scale	Incidence[2] scale	Underlying scale	Incidence[2] scale	Economic response of breeding objective (per cow)[3]
Both traits not in index and objective	0.019	-0.56%	-0.0095	0.29%	0
Both traits in index and objective	0.015	-0.46%	-0.0084	0.25%	+£0.11
Only CEd in index and objective	0.014	-0.45%	-0.0086	0.26%	+£0.09
Only CEd in restricted index and objective	0	0	-0.0026	0.08%	-£0.54

[1] CEd = direct calving ease, CEm = maternal calving ease
[2] % less severe or worse calvings per generation
[3] Relative to the current breeding objective (without calving ease)

Table 6.2 Effect of the genetic direct-maternal correlation on response in calving ease when the trait is in the index and breeding objective

Trait[1]	CEd		CEm		
Genetic correlation	Underlying scale	Incidence[2] scale	Underlying scale	Incidence[2] scale	Economic response of breeding objective (per cow)[3]
0.00	0.016	-0.49%	-0.0098	0.29%	+£0.13
-0.10	0.015	-0.47%	-0.0094	0.28%	+£0.12
-0.50	0.014	-0.45%	-0.0081	0.24%	+£0.10

[1] CEd = direct calving ease, CEm = maternal calving ease
[2] % less severe or worse calvings per generation
[3] Relative to the current breeding objective (without calving ease)

6.1.3. What can we do to improve genetic progress in calving traits?

6.1.3.1 Recommendations to the industry

Data of good quality, hence with minimal error, is essential for genetic evaluation. Studies in this thesis were provided with a dataset consisting of national field data in large quantity. Phenotypic information was collected by two major milk organisations and subsequently merged. The available data yielded sufficient quality data for the purposes of routine genetic evaluation of calving ease. However, calving traits are complex traits for genetic selection and several changes to the data recording of these traits can considerably enhance future genetic evaluation. The recommendations to improve data recording on calving ease and stillbirth that have arisen from this thesis work are:

- Develop a single, well defined, scoring scale for use by both milk recording organisations. This will considerably minimise subjectivity in scores and avoids an additional step in data editing which might introduce error.
- Record the sex of the stillborn calf. Gender is a major factor affecting stillbirth, therefore it *must* to be concluded in the statistical model to avoid bias and increase precision in the estimated breeding values for this trait.
- Implement a more objective recording scale for the birth weight of the calf. Literature suggests a high correlation between calving traits and birth weight. Therefore the inclusion of a well recorded birth weight trait can enhance the predictive ability of the statistical model and aid considerably in the understanding of the genetic relationships between calving ease, stillbirth and gestation length. Currently, the indicator trait of gestation length can improve

accuracy of proofs for both calving traits. Yet, birth weight is expected to serve this purpose better.

- Record whether or not the calving event was observed. This information is not routinely recorded and therefore there is a risk that farmers record an unobserved calving as easy and thus 'easy' category is in fact a pool of true easy calvings and unobserved calvings of varying difficulty which fortunately resulted in a healthy cow and calf.

6.1.3.1.1 Recommendations for the communication of calving traits

One of the themes in this thesis is the emphasis on the complex nature of calving traits. Through this thesis work, and through personal communication, it has become apparent that calving traits are generally misunderstood. The direct and maternal genetic components which make up the phenotype of a calving or stillbirth combined with the separate environmental components confuse almost anyone who gets involved with these traits. Yet, in order to make sustainable genetic improvement in the traits, they must be understood; completely. I hereby refer to both the direct and maternal component and *especially* the relationship between these components. This starts with the acknowledgement of parturition as a tight collaboration between offspring and dam. The recorded phenotype is a result of many physiological processes in both foetus and dam (Senger, 2003) and thus *both* individuals are affected by an undesirable parturition, which is clearly shown by Chapter 2. The direct and maternal genetic components are separated at analysis yet come from a single observation, are correlated and are expressed in the same lifetime of a female. Acknowledgement of this can only benefit genetic progress, as shown in all chapters of this thesis. It is therefore a strong recommendation to the industry to ensure that

all parties which are involved in any part of communication regarding calving traits understand the phenotypic make-up of a calving trait, how genetic parameters are estimated (separating both genetic components from a single observation) and what consequences selection might have (negative direct-maternal genetic relationship). This is regardless of the type of communication e.g. progeny data recording, breeding advice or veterinary advice. If it is not well explained that selection upon either a direct or a maternal calving trait should thus always follow consultation of genetic merit on the other trait, then genetic progress will be considerably hampered. Further advice on how breeding values could be communicated in order to minimise confusion and help selection advice is given in the next section.

6.1.4. Lessons from current developments in animal breeding

6.1.4.1. Maternal effects vs. associative effects

In this thesis (Chapter 1 and 3) I have explored the concept of a total heritable variance as suggested in work on associative effects. Although first defined by Griffing (1967), attention for how group members affect the phenotype of a focal individual has rapidly increased since Muir and Bijma et al. have taken to the field.

In a trait affected by associative effects, each individual may affect both itself and the individuals it associates with (Bijma et al. 2007). Following this definition, there is a clear resemblance between associative effects and maternal effects. It is therefore interesting to put maternal effects side by side with associative effects to explore similarities and differences. As such, one can evaluate if and where genetic progress in maternal traits can benefit from the research currently done on associative effects. As the focus of this thesis lies with making genetic progress in calving traits, this

section will mainly address the potential of associative and maternal effects to contribute to response to selection.

Maternal effects and associative effects can be schematically explained as Figure 6.1.

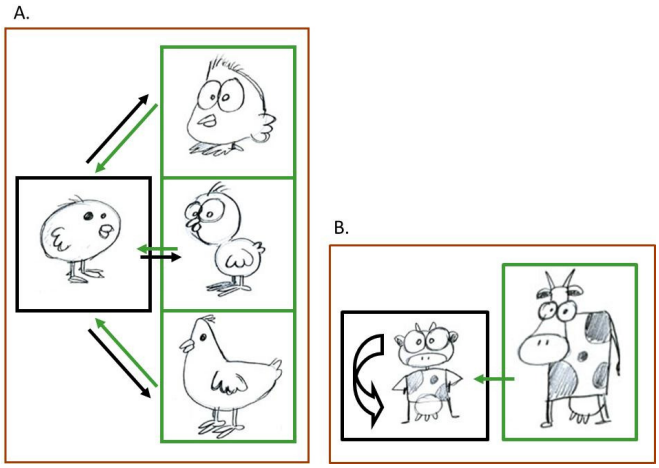


Figure 6.1 Diagram presenting two situations in which A. associative effects and B. maternal effects affect the phenotype of focal individual i alongside the direct effect.

where situation **A.** represents the interaction between associates kept together in a 'group' (here a flock of chickens, picture by Katrijn Peeters) where the phenotype of individual i is influenced by the social effects of its associates. Situation **B.** describes the phenotype of a focal individual i in cattle, in which the maternal effect expressed by the dam of i has an effect on its phenotype as described in Chapter 1.

The phenotypes of i in Figure 1 for **A**. and **B.** are:

$$\boldsymbol{A}.\ P_i = A_{\boldsymbol{D,i}} + E_{\boldsymbol{D,i}} + \sum A_{S,j} + \sum E_{S,j}\ ,\ \boldsymbol{B}.\ P_i = A_{D,i} + E_{D,i} + A_{M,j} + E_{M,j} \qquad [6.4]$$

where in equation **A.** j is an associate individual in the group of i and As and Es represent the additive and environmental associative effect respectively and equation **B.** describes the phenotype of a maternal trait as modelled by Willham (1963) (Chapter 1). As both maternal effects and associative effects are additive, they can

respond to selection alongside direct genetic effects. The population mean for a trait that is affected by associative effects is then described by Bijma et al. (2007) as

$$\bar{P} = \left(\frac{1}{m}\right)\sum_m P_i = \left(\frac{1}{m}\right)\left[\sum_m P_{D,i} + (n-1)\sum_m P_{S,i}\right] = \bar{P}_D + (n-1)\bar{P}_S \quad [6.5]$$

where m is population size and n is group size.

Following this decomposition of the population mean, total genetic response per generation is then for **A.** the increase of the direct breeding value DBV and (n-1) IDV (indirect, or associative, breeding value)

$$A.\,\Delta\bar{P} = \Delta A_D + (n-1)\Delta A_S \quad [6.6]$$

According to classical animal breeding theory, response to selection equals the per generation change of the direct breeding value. In traits affected by indirect genetic effects however, there is the additional change of the indirect breeding value. According to Bijma et al. (2007) one would therefore expect that the breeding value of an individual for traits affected by associative effects is equivalent to $A_d + (n-1)A_s$ which is referred to as the Total Breeding Value (TBV) by Bijma et al. (2007) as also described in Chapter 3. Response to selection would then equal the per generation change of the TBV. The definition of a breeding value of an animal under random mating is defined as (Bruce and Walsh, 1998): *'2x (the expected deviation of its offspring mean phenotype from the population mean)'*. In equations $\Delta\bar{P} = \Delta A_D + (n-1)\Delta A_S$ and $A_D + (n-1)A_S$ the indirect (associative) breeding value (IBV) is multiplied by a factor of (n-1) as it is assumed that the IBV will be expressed a number of times relative to the number of group members. Or, the expected performance of the animals' offspring to which the TBV belongs is dependent on the number of times it is expressed which is assumed to be the same number of

individuals the animal associated with and could be argued as is a form of genotype by environment (GxE) interaction.

If we now extend the theory on associative effects to a maternal effects situation, then the population mean would be described as

$$\bar{P} = \left(\frac{1}{m}\right)\sum_m P_i = \left(\frac{1}{m}\right)\left[\sum_m P_{D,i} + \sum_m P_{M,i}\right] = \bar{P}_D + \bar{P}_M \quad [6.7]$$

and response to selection, or change in population mean would equal

$$B.\Delta\bar{P} = \Delta A_D + \Delta A_M \quad [6.8]$$

This is where the maternal effects situation differs from the associative effects situation as it lacks the multiplication factor n. The phenotype for a maternal trait is the result of a single interaction e.g. that of offspring with dam, as opposed to that for an associative trait which is the result of multiple interactions of the focal individual with its associates. The TBV of an animal for a maternal trait as described in Chapter 3 would then be $A_D + A_M$. Am does not get multiplied by the number of times it is expressed, as As does, despite that it might be expressed multiple times when, in the example of calving ease, a cow calves multiple times. Or the maternal breeding value is not affected by the number of times the animal has calved. This is different for a maternal effect trait for animals that have single litters with multiple offspring as then the maternal effect *is* expressed n times, where n is litter size. The expected performance of offspring, following the theory by Bijma et al. would then be dependent on n and the TBV would equal $A_D + nA_M$. Response to selection would then also no longer equal the per generation change of the TBV. The total heritable variation on which selection decisions can be made, following Bijma et al. would for associative traits and maternal traits be equal (the latter described in Chapter 1 and used in Chapter 3 and 4) and is

$A.\sigma^2_{TBV} = \sigma^2_{A_D} + 2(n-1)\sigma_{A_{DS}} + (n-1)^2\sigma^2_{A_S}, B.\sigma^2_{TBV} = \sigma^2_{A_D} + 2\sigma_{A_{DM}} + \sigma^2_{A_M}$ [6.9]

Associative effects have brought new insight into indirect genetic effects and show the importance of its contribution to response to selection. However, considering that they differ at some crucial points, it is important to keep maternal effects and associative effects separate so that confusion is avoided. I would therefore suggest not to term maternal effects as associative effects but to list both as different indirect genetic effects. It has already been discussed in Chapter 3 that the TBV and its variance, originating from work by Muir and Bijma, find value in explaining the importance of considering both direct and maternal effects to AI organisations and farmers. It would however not be the TBV but an aggregate index value, representing the contribution of selection of the potential sire to the genetic gain of the trait that can aid in making genetic progress as it will incorporate the negative direct-maternal covariance (Chapter 3). In this aggregate index value, the maternal breeding value must be multiplied by the number of times it is expressed which makes it different from the TBV. An assumed parameter equal to the UK average lifetime number of times a cow calves may be used to generate this index value. It would then equal $A_D + 0.8 * 0.5(nA_M)$ considering 50% chance of a bull calf which is assumed not to be kept for breeding and 80% probability of a female offspring to become a replacement heifer.

6.2. Conclusions

This thesis evaluated the feasibility of genetic selection on calving traits in UK Holstein-Friesian dairy cattle using national data on single calvings. It provided increased insight into the importance, methodology and consequences of genetic

selection for calving ease and reduced stillbirth. Short term and long term adverse effects were determined after a difficult calving on the profitability of the dairy farm. Detrimental effects on milk production were even larger for the dairy calf than the dairy cow, which is new and important information for the dairy cattle industry.

This work confirmed well-known problems in the estimation of genetic parameters for maternal effects. It showed that genetic variation in calving traits is low but detectable. However, analyses proved that acknowledgement of the calving trait as being of maternal nature, with all its complex characteristics, improves ultimate accuracy of parameters and thus increases potential genetic progress. A multi-trait sire-mgs model was recommended for genetic analyses while genomic analyses benefit from a multi-trait genomic prediction model where direct and maternal components are assumed to be related.

This thesis also clarified genetic relationships between calving ease, gestation length and other traits of which most are included in the national genetic index, PLI. Estimation of both direct and maternal correlations between traits gave new insight into potential consequences of selection and allows the inclusion of calving ease in the national genetic index and breeding objective.

This thesis ultimately shows that genetic selection on calving traits is feasible and, given the national prevalence, highly desired. Genetic progress can however be maximised by collaboration between organisations involved in data recording such that data quality is enhanced, by careful consideration of the genetic direct-maternal relationship in all conducted analyses and all selection decisions and by emerging developments in animal breeding such as genomic selection.

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Appendix A: Sire (co)variances to direct and maternal (co)variances

A.1. Within traits:

Calving traits:

Direct:

$A_D = 2 * sire.calf,$

$sire.calf = \frac{1}{2} A_D,$

$\sigma^2_{A_D} = 4 * \sigma^2_{sire.calf},$

Maternal:

$A_M = 2 * sire.cow - sire.calf,$

$sire.cow = \frac{1}{2} A_M + \frac{1}{4} A_D,$

$\sigma^2_{A_M} = 4 * \sigma^2_{sire.cow} + \sigma^2_{sire.calf} - 4 * \sigma_{sire.calf,sire.cow},$

Direct-maternal covariance:

$Cov(A_D, A_M) = Cov(2sire, 2mgs - sire), \sigma_{A_{dm}}$
$= 4 * \sigma_{sire.calf,sire.cow} - 2 * \sigma^2_{sire.calf}$

All other traits:

Direct:

$sire.cow = \frac{1}{2} A_D,$
$A_D = 2 * sire.cow,$
$\sigma^2_{A_D} = 4 * \sigma^2_{sire.cow}$

A.2. Between traits:

Example:

Trait 1: Calving ease, Trait 2: Calving Interval

Direct 1 – Direct 2:

$Cov(A_{D\_1}, A_{D\_2}) = Cov(2 * 1\ \_sire.calf, 2 * 2\ \_sire.cow) = 4 * \sigma_{A_{1\_sire.calf,2\_sire.cow}}$

Maternal 1 – Direct 2:

$Cov(A_{M\_1}, A_M) = Cov(2 * 1\ \_sire.cow - 1\ \_sire.calf, 2 * 2\ \_sire.cow$
$= 4 * \sigma_{A_{1,2\ \_sire.cow}} - 2 * \sigma_{A_{1\ \_sire.calf,2\ \_sire.cow}}$